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Robbin C. Moran

Volume 34, Article 1
November 1987

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Robbin C. Moran

Illinois Natural History Survey
Illinois Department of Energy and Natural Resources

Department of Plant Biology
University of Illinois at Urbana-Champaign

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This work is dedicated to my parents, Livia Ann Moran and John Howard Moran.

Dr. Robbin C. Moran currently works at the Missouri Botanical Garden in St. Louis.

Illinois Natural History Survey, Lorin I. Nevling, Chief
A Division of the Illinois Department of Energy and Natural Resources

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This work was originally part of a dissertation submitted to the Graduate College of the University of Illinois at Urbana-Champaign in partial fulfillment of the requirements for the degree of Doctor of Philosophy in plant biology.

Monograph of the Neotropical Fern Genus *Polybotrya* (Dryopteridaceae)

Robbin C. Moran

Part One: Introduction and Discussion

The need still is for more monographic work on tropical species, which represent the great majority of all ferns.

R.E. Holttum (1982)

The genus *Polybotrya* (Dryopteridaceae) includes 35 species of neotropical ferns. It is distinguished by 1) strongly dimorphic leaves with fertile leaves that resemble skeletons of the sterile, photosynthetic ones; 2) usually high-climbing stems that are covered with scales; and 3) a unique stem anatomy with 5 to 12 circularly arranged meristeles, each surrounded by a black sclerenchymatous sheath, with numerous tiny leaf traces arching between adjacent meristeles. The center of diversity of the genus is the Andes, where 23 species occur, 12 of which are endemic. The coastal mountains of southeastern Brazil are notable because they contain 5 species, all endemic. The range of *Polybotrya* is from Chiapas, Mexico, southward through Central America; the West Indies; northern South America southward along the Andes to Bolivia and Paraguay and eastward to the Guiana Highlands; the Amazon River basin and the Matto Grosso; and southeastern Brazil. Species of the genus typically inhabit wet, shaded, primary tropical forests from sea level to 2500 m, most often occurring at middle altitudes between 500 and 2000 m.

Polybotrya is divided into three subgenera: 1) *Soromanes*, leaves simply pinnate and veins anastomosing; 2) *Sorbifolia*, leaves simply or twice pinnate and veins free, close, and parallel; and 3) *Polybotrya*, leaves decompound and veins free. *Polybotrya cervina*, a species usually included in *Polybotrya*, is removed to the monotypic genus *Olfersia* (Moran 1986). *Polybotrya* is related to dryopteroid genera such as *Arachniodes*, *Cyclodium*, *Maxonia*, *Olfersia*, and *Polystichopsis*. Carl Christensen, the father of modern fern taxonomy, observed (1916) that *Polybotrya* may have arisen from *Maxonia* because both have high-climbing stems and strongly dimorphic leaves. The morphological and anatomical evidence presented here suggests that *Polybotrya* may have evolved instead from a *Cyclodium*-like ancestor.

I chose *Polybotrya* for study because two aspects of the genus immediately intrigued me: its strongly differentiated sterile and fertile leaves and its long, creeping hemiepiphytic stem (Fig. 1). Since these features evolved separately in unrelated fern genera, studying *Polybotrya* might well provide insight into broader questions of fern evolution. *Polybotrya* was suited to monographic study because the number of species (35), all of which are neotropical, was manageable. Finally, no previous monographic work had been done on *Polybotrya* and many problems of nomenclature and identification remained to be solved.

Materials and Methods

This monograph is based on the study of about 2500 herbarium sheets, which represent approximately 800 individual collections from 30 herbaria (see acknowledgments). Unfortunately, *Polybotrya* at Kew could not be examined because their policy precludes loaning specimens for use by graduate students (G.L. Lucas, *in litt.* 1983; pers. comm.). Kew, however, did send color slides of several critical type specimens.

FIGURE 1. Habit sketches for two species of *Polybotrya*. Above, *P. crassirhizoma*, a climbing species; below, *P. sorbifolia*, a terrestrial species. Note that the fertile leaves are skeletonlike and that their orientation is more erect than that of the spreading sterile leaves.

I spent seven months observing and collecting 18 of the 35 species of *Polybotrya* in Costa Rica, Ecuador, Peru, and Venezuela and was able to make such important observations about the biology of the species as presence of aerophores and mucilage on stems, duration and habit of sterile versus fertile leaves, and variation within and between populations. During field work, herbarium, cytological, and anatomical materials were also collected.

Anatomical cross sections were prepared by freehand sectioning, and staining was rarely needed to determine cell types or tissue layers. Leaf segments were cleared by soaking them in 10 percent NaOH in a warm oven for 5 to 6 days. Several changes of clearing solution were usually needed to replace solution that had become darkly stained by phenolic substances. Since this procedure did not remove all the dark color from the leaf, the segments were placed in full-strength Clorox bleach from 10 to 60 minutes. This treatment usually rendered even the most stubborn leaves translucent for microscopic study.

Taxonomic History of the Genus

Polybotrya was first described by Willdenow in his fourth edition of Linnaeus's *Species Plantarum* (1810), as distinguished by "Capsules sessile, globose, aggregated in naked paniculate spikes. Nonindusiate" [my translation]. *Polybotrya osmundacea*, the sole species described in the new genus, received its specific epithet because of the fancied resemblance of its fertile leaf with the fertile leaf apex of *Osmunda regalis*. Since strongly contracted, nonindusiate fertile leaves were considered the principal feature of the new genus, other species with similar leaves were eventually placed in *Polybotrya*. Since fully differentiated fertile leaves have arisen separately along many phyletic lines, this procedure resulted in a highly unnatural, polyphyletic genus. Species placed in *Polybotrya* at one time and then excluded are represented today in as many as 12 genera (see Excluded Taxa).

Past Generic Concepts

Each of the nineteenth-century pteridologists who wrote about *Polybotrya* had a slightly different concept of the genus (Table 1). Blume (1828) placed many unrelated acrostichoid ferns, including species of *Lomagramma*, *Stenosemia*, and *Bolbitis*, in *Polybotrya*. Schott (1834–1836) later restricted *Polybotrya* to the American species allied to *P. osmundacea*. The subsequent recognition of the Asian acrostichoids as distinct from the American genus *Polybotrya* testifies to Schott's keen perception. Although Schott's classification was not immediately adopted by his colleagues, it was eventually revived by Smith (1875) and Christensen (1934).

Presl (1836) relied heavily on venation patterns and anatomical characters in defining his genera and did not accept Schott's circumscription of *Polybotrya*. He merged species of *Bolbitis* sect. *Egenolfianae* with *Polybotrya* because both had free veins, but he removed the anastomosing-veined species placed in *Polybotrya* by Blume (1828).Smith (1841) largely followed this classification in his arrangement of fern genra.

Fée (1845) was the first pteridologist to try to make sense out of the increasing number and diversity of acrostichoid ferns. He included the species related to *P. osmundacea* in his subgenus *Eupolybotrya* and created two subgenera of *Polybotrya* (see Excluded Taxa) in which he put many species now placed in *Bolbitis*, *Blechnum*, *Lomariopsis*, and *Teratophyllum*. Fée also erected the segregate genus *Soromanes* for species of *Polybotrya* with anastomosing veins and 1-pinnate leaves. In my treatment, *Soromanes* is a subgenus of *Polybotrya*.

The German pteridologist Mettenius had a wide circumscription of *Polybotrya*. He described several new species in the genus, some of which are here retained. The majority, however, have been placed in *Bolbitis*, *Elaphoglossum*, and *Leptochilus*.

Hooker (1864: 194–195) and Baker in Hooker and Baker (1874: 399ff.) subsumed both *Polybotrya* and *Soromanes* as subgenera in their large, eclectic genus *Acrostichum*,

which consisted of any fern with acrostichoid sori. This decision was essentially a reversion to Swartz's (1806) concept of *Acrostichum*, and although both genera were recognized as subgenera, *Polybotrya* continued to include unrelated species that have since been placed in *Atalopteris*, *Elaphoglossum*, *Psomiocarpa*, and *Teratophyllum*. Hooker and Baker's classification was accepted by several pteridologists, especially by flora writers, until the hegemony of Hooker's concepts was supplanted by the more natural views of Smith (1875). Smith accorded generic status to *Polybotrya*, restricting it to *P. osmundacea* and its immediate allies; however, he kept *Soromanes* as a distinct genus.

Unfortunately, Smith's views were not immediately accepted by pteridologists. Christ (1897) and Diels (1899) classified many of the acrostichoids with free veins in *Polybotrya*, a decision that again resulted in an amalgamation of unrelated species. Christensen (1905) in *Index Filicum* used *Polybotrya* at the rank of genus, but it had essentially the same circumscription as it had had under Hooker. Unlike the writers cited above, he placed *Olfersia cervina* in *Polybotrya*. His classification was used by Schumann (1915) in her important work on the vascular supply in fertile leaves of acrostichoid ferns. Christensen (1934) later removed the discordant species from *Polybotrya* and placed most of them in the genera where they are found today (*Atalopteris*, *Egenolfia*, *Lomagramma*, and *Psomiocarpa*).

Copeland's *Genera Filicum* (1947) adopted Christensen's earlier (1905) concept. Pichi-Sermolli (1977) treated *Polybotrya*,

TABLE 1. Comparative treatment of *Polybotrya*.

Reference	*Polybotrya* subgenus *Soromanes**	*Polybotrya* subgenus *Sorbifolia**	*Polybotrya* subgenus *Polybotrya**	Genera formerly included in *Polybotrya*
Willdenow (1810)			*Polybotrya*	
Kaulfuss (1824)			*Polybotrya*	*Olfersia*
Blume (1828)			*Polybotrya*	*Bolbitis, Lommagramma, Stenosemia*
Schott (1834–1836)			*Polybotrya*	
Presl (1836)			*Polybotrya*	*Bolbitis*
Smith (1841)			*Polybotrya*	*Bolbitis*
Fée (1845)	*Soromanes*		*Polybotrya* subgenus *Eupolybotrya*	*Blechnum, Bolbitis, Lomariopsis, Teratophyllum*
Hooker (1864)	*Acrostichum* subgenus *Soromanes*	*Acrostichum* subgenus *Polybotrya*	*Acrostichum* subgenus *Polybotrya*	*Atalopteris, Psomiocarpa, Teratophyllum*
Smith (1875)	*Soromanes*	*Polybotrya*	*Polybotrya*	
Christensen (1905)	*Polybotrya*	*Polybotrya*	*Polybotrya*	*Atalopteris, Bolbitis, Olfersia, Psomiocarpa, Teratophyllum*
Christensen (1934)	*Polybotrya*	*Polybotrya*	*Polybotrya*	
Copeland (1947)	*Polybotrya*	*Polybotrya*	*Polybotrya*	*Olfersia*
Pichi-Sermolli (1977)	*Soromanes*	*Polybotrya*	*Polybotrya*	
Tryon & Tryon (1982)	*Polybotrya*	*Polybotrya*	*Polybotrya*	*Olfersia*

* refers to the treatment of the genus in this work.

Soromanes, and *Olfersia* as distinct genera but placed *Soromanes* and *Polybotrya* on separate branches of his phylogenetic diagram. Tryon and Tryon (1982) are the most recent authors to discuss *Polybotrya* and related genera; their concept is like that used in the present work, except that they include *Olfersia cervina* in *Polybotrya*. In the present monograph, I restrict *Polybotrya* to the species allied closely to *P. osmundacea*, make *Soromanes* a subgenus of *Polybotrya*, and keep *Olfersia cervina*, which has been placed in *Polybotrya* by many recent pteridologists, in its own monotypic genus. I recognize 35 species of *Polybotrya*, all of which are neotropical and 10 of which are new.

Work at the Species Level

The species of *Polybotrya* have received less study over the years than those of most other fern genera. Fée (1845), Hooker (1864), and Hooker and Baker (1874) have been the only monographers of the genus. Although they attempted to identify all of the then-known species of *Polybotrya*, they did not always see types, overlooked several published names, put some species in synonymy without adequate study, and did not make detailed observations on the genus because they were studying hundreds of other ferns at the same time. Despite these shortcomings, the works of these three men have been the best source for identifying specimens of *Polybotrya* in many regions of tropical America.

The difficulty of identifying specimens of *Polybotyra* has been partially alleviated by local or regional floras, but these cover only a limited portion of the geographic range of the genus and are often incomplete. In many of these floras, types were rarely examined and names, therefore, were often applied incorrectly. Only Sodiro's (1897) treatment of the ferns of Ecuador is available for the Andean region; yet he was aware of only 6 of the 23 species that occur in that region. Vareschi's (1969) treatment for Venezuela and Brade's (1971) for Brazil have helpful illustrations, but the names are often misapplied. The best treatment of *Polybotrya* for Mesoamerica is Stolze's (1981) excellent work for the *Flora of Guatemala*, but Guatemala lacks several species found in Mesoamerica. In brief, adequate keys and descriptions are lacking for identifying *Polybotrya* throughout most of its range and, as a result, many specimens have been misidentified.

In this century, most of the research on *Polybotrya* has focused on the specific level. Brade (1935, 1948) described two new species of *Polybotrya* in papers that included other ferns as well. Later, in a series of three papers published in the Brazilian journal *Bradea* (1969a,b,c), he described ten additional new species from Brazil, Costa Rica, and Venezuela. These papers were based on field studies in the American tropics, and most of the types were plants he had collected by himself or with his brother Alfred. Brade (1971) published a synopsis providing keys and illustrations of the Brazilian species of *Polybotrya*. Unfortunately, he died before completing the descriptions, habitats, and distributional information. Only five of Brade's names are accepted in this monograph as representing valid species; the remainder are relegated to synonymy.

More recently, Lellinger (1972, 1977) published two important papers on *Polybotrya*. In the first, he described five new species from South America and offered interesting ecological notes on the genus. In the second, which deals with other ferns as well, he described two new species that are endemic to Colombia. Only three of these seven species are accepted here. About half of the species described by Brade and by Lellinger have, therefore, been relegated to synonymy in the present work, largely because I found older, obscure names during my research. In some cases, these names had not been used since their original publication. The proliferation of names is one of the pitfalls faced by taxonomists when synthetic or revisionary works are unavailable for a group and in this case indicates how much *Polybotrya* has needed a monograph.

Ecology

Polybotrya inhabits wet, shaded, tropical forests. These may be hot, humid, lowland rain forests or cool, cloud forests at high elevations. The genus rarely occurs in disturbed forests, and when it does, it is represented by only a few isolated plants. However, small scale disturbances within mature forest, such as light gaps created when a huge tree dies, appear to be important in establishing young plants (Lellinger 1972). During fieldwork in tropical America, I never observed young sporophytes or their associated gametophytes establishing themselves on roadbanks or on shaded, disturbed slopes adjacent to roads. Furthermore, all herbarium specimens that contained habitat information listed only primary forest as the habitat. The restriction of *Polybotrya* to wet, shaded, primary, tropical forest is reflected by its geographic distribution (Fig. 2a). The genus is absent from such arid regions as central Mexico and the western coast of Peru and from such nonforested regions as the Llanos of Venezuela and Colombia (Figs. 2a & 3). The altitudinal range of *Polybotrya* is from sea level to 2500 m, with most plants collected from 500–2000 m (Fig. 4). This range certainly corresponds to my field observations that *Polybotrya* is most diverse, frequent, and abundant at middle elevations.

FIGURE 2. Distribution of *Polybotrya*. a. composite of Maps 1–21; b. number of species (left bar), number of endemics (right bar). Countries or areas are outlined; those with only one bar have no endemics. See Table 3 for numbers of taxa in each country.

Geography

In the following discussion, the distribution of *Polybotrya* is given according to the regional centers defined by Tryon (1972). These regional centers, all mountainous, were determined by their high endemism and species richness.

The most important regional center in the diversification of *Polybotrya* is the Andean, from Venezuela and Colombia south to Bolivia (Fig. 2b, Table 2). The Andean Region contains 23 species, 12 of which are endemic, and I suspect that new species of *Polybotrya* will be found there. Within this region, Colombia contains the richest *Polybotrya* flora: 17 species, 6 of which are endemic (Table 3). The coastal mountains of northern Venezuela contain *P. canaliculata* and *P. serratifolia*, both occurring in cloud forests from 1200–2400 m. *Polybotrya canaliculata* has a very limited distribution and is a true endemic to the coastal mountains (Map 19); it occurs outside of the Andean Region as defined by Tryon (1972). *Polybotrya serratifolia* is considered a near-endemic, extending southwest into the Andes around Mérida and eastward to Trinidad (Map 1).

The Serra do Mar Mountains of the Southeastern Brazilian Region contain five species

FIGURE 3. Distribution of *Polybotrya* species within regional centers of diversity and endemism for tropical American ferns defined by Tryon (1972). Primary centers are indicated with dark shading; secondary centers, with light shading. The number on the left is the total number of species; the number in parentheses indicates how many of those species are endemic. See Table 4 for comparisons.

of *Polybotrya*, all of which are endemic (Fig. 3, Tables 2 & 3). I find it remarkable that this region has no species of *Polybotrya* in common with those of the other regional centers (Table 4) or with intervening areas. This distinctiveness of the *Polybotrya* flora is accentuated by its lack of the simply pinnate species, that is, subgenera *Soromanes* and *Sorbifolia*. The biogeography of *Polybotrya* strongly supports data from many other sources that suggest that the isolated Serra do Mar Mountains are a distinctive biogeographic center (Tryon 1972).

Only one species, *P. goyazensis*, occurs in the Matto Grosso and intervening area between the Andean and Brazilian regional centers (Map 6). This species is closely related to the widespread *P. caudata* and is probably an example of the peripheral "budding" of a new species from the southern part of the range of *P. caudata*.

The Amazon basin contains one endemic, *P. glandulosa*, which has been collected only three times (Map 7). Most species of *Polybotrya* in the Amazon basin also grow in the Andean Region. In contrast, the coastal mountains of southeastern Brazil have contributed no species to the Amazonian lowlands. My field experience in the Amazon basin of Ecuador and Peru showed that in forests on wet, sandy soils *P. caudata* was common; forests on lateritic soils, however, had *P. crassirhizoma*, *P. caudata*, *P. osmundacea*, and *P. pubens*. All five species were abundant in the western Amazon basin where I collected, and I suspect that they extend farther eastward into the Amazon basin than is shown on their range maps.

The Guiana Highlands Region does not contain a distinctive *Polybotrya* flora. Only six species occur there and most of these are widespread elsewhere. The region, therefore, has a high floristic affinity with the Andean and Central American regional centers (Table 4). *Polybotrya sessilisora*, which occurs in the Guiana Highlands and in the adjacent Amazon basin (Map 20), is probably more common in the Highlands and its range may be centered there. *Polybotrya* has two notable examples of Andean-Guianan range disjunc-

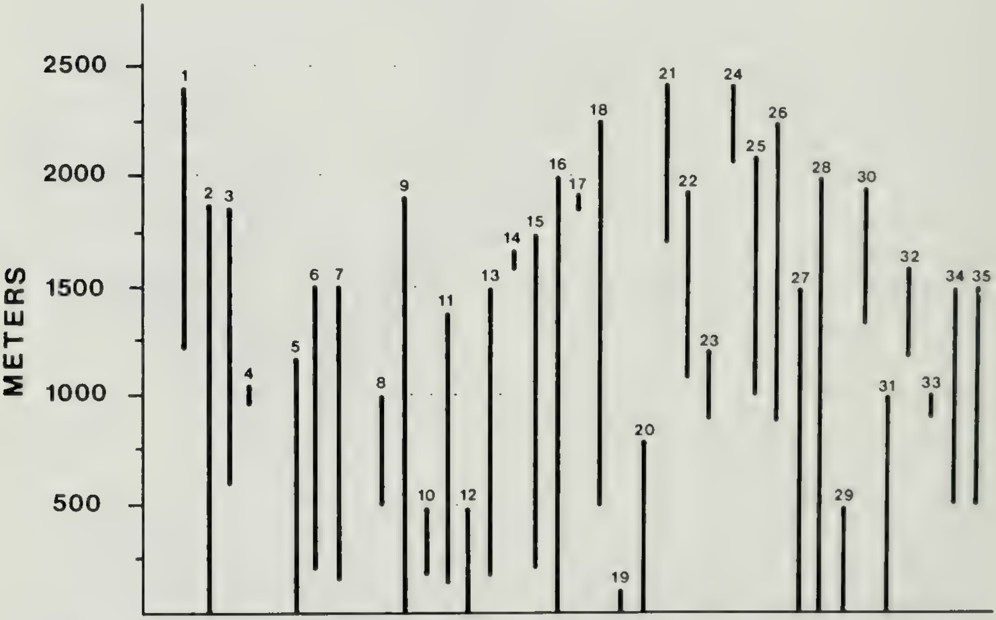

Figure 4. Altitudinal ranges of *Polybotrya* species. The numbers above the bars correspond to the species numbers assigned in the taxonomic treatment.

tions. The first example, *P. lechleriana*, is known in the Guianas from a single collection at Mount Roraima in Guyana, 1900 km from its nearest locality in Colombia (Map 7). This disjunction is probably best explained by long-distance spore dispersal from Andean populations. The second example, *P. fractiserialis*, occurs primarily in the foothills of the Andes and is disjunct in the southern Pakaraima Mountains of British Guiana, 2000 km from the nearest Andean population in Ecuador. Unlike *P. lechleriana, P. fractiserialis* is common and widespread in the Guianas (Map 3).

The Central American Region contains seven species, including one endemic (Fig. 3, Table 2). All seven species occur in Costa Rica (Table 3). My fieldwork there showed that *P. polybotryoides, P. osmundacea, P. alfredii* and *P. gomezii* (endemic) were particularly common in the mountains and that *P. caudata* was frequent in the costal lowlands. *Polybotrya alfredii* and *P. gomezii* were particularly abundant in cloud forests, often growing together. In the mountains of central Panama, just outside the Central American Region as defined by Tryon (1972), one endemic occurs, *P. alata*.

The Greater Antilles Region, otherwise quite rich in fern species, has only one *Polybotrya* species, the widespread *P. osmundacea* (Figs. 2 & 3, Table 2). Puerto Rico lacks *Polybotrya* but certainly has suitable forest habitat. In the Lesser Antilles, *P. osmundacea* is found on Grenada. Martinique and Guadeloupe have the closely related endemic *P. cyathifolia*. The Caribbean islands have played a minor role in the diversification of *Polybotrya*.

Polybotrya caudata and *P. osmundacea* clearly have the largest geographical and altitudinal ranges of any species in the genus (Maps 5 & 18). With the exception of southeastern Brazil, these two species extend nearly throughout the entire area covered by all of the other species in the genus.

Polybotrya occurs on only one oceanic island—Cocos Island, about 500 km (310 mi) southwest of Costa Rica in the Pacific Ocean. Three species occur there: *P.*

TABLE 2. The geographic regions shown in Figure 3 and the species of *Polybotrya* that occur in them.

Geographic Region (after Tryon 1972)	Species (numbers correspond to those in the taxonomic treatment)	No. in Region (% of total species in genus)	No. Endemic (% for region)
Greater Antilles	28	1 (3)	0
Lesser Antilles	28; 29	2 (6)	1 (50)
Mexican		0	0
Mexican–Central American	2,9	2 (6)	0
Central American	2, 3, 5, 9, 16, 27, 28	7 (20)	1 (14)
Central American–Andean	2, 3, 9, 16, 23, 28	6 (17)	1 (17)
Andean	1, 2, 3, 4, 5, 6, 7, 9, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21, 22, 24, 25, 26, 28, 30	23 (66)	12 (52)
Andean–Guianan	1, 5, 7, 9, 11, 12, 28, 31, 32	9 (26)	1 (11)
Guianan	5, 6, 9, 13, 28, 31	6 (17)	0
Guianan–Southeast Brazilian	5, 7, 9, 10, 11, 12, 31	7 (20)	0
Southeast Brazilian	10, 20, 33, 34, 35	5 (14)	5 (100)
Southeast Brazilian–Andean	10	1 (3)	0

TABLE 3. Distribution of *Polybotrya* by country. Endemics are in boldface. Numbers in parentheses refer to the species numbers assigned in the taxonomic treatment.

MEXICO: 2 species, no endemics. *polybotryoides* (2), *caudata* (9).

BELIZE: 2 species, no endemics. *polybotryoides* (2), *caudata* (9).

GUATEMALA: 3 species, no endemics. *polybotryoides* (2), *caudata* (9), *osmundacea* (28).

HONDURAS: 3 species, no endemics. *polybotryoides* (2), *caudata* (9), *osmundacea* (28).

NICARAGUA: 3 species, no endemics. *caudata* (9), *alfredii* (16), *osmundacea* (28).

COSTA RICA: 6 species, 1 endemic. *polybotryoides* (2), *sorbifolia* (5), *caudata* (9), *alfredii* (16), **gomezii** (27), *osmundacea* (28).

COCOS ISLAND: 3 species, no endemics. *polybotryoides* (2), *caudata* (9), *osmundacea* (28).

PANAMA: 5 species, 1 endemic. *polybotryoides* (2), *caudata* (9), *alfredii* (16), **alata** (23), *osmundacea* (28).

CUBA: 1 species, not endemic. *osmundacea* (28).

JAMAICA: 1 species, not endemic. *osmundacea* (28).

HAITI: 1 species, not endemic. *osmundacea* (28).

GUADELOUPE & MARTINIQUE: 1 endemic. **cyathifolia** (29).

GRENADA: 1 species, not endemic. *osmundacea* (28).

TRINIDAD: 3 species, no endemics. *serratifolia* (1), *caudata* (9), *osmundacea* (28).

FRENCH GUIANA: 3 species, no endemics. *fractiserialis* (6), *caudata* (9), *osmundacea* (28).

SURINAM: 2 species, no endemics. *fractiserialis* (6), *caudata* (9).

GUYANA: 4 species, no endemics. *fractiserialis* (6), *caudata* (9), *lechleriana* (13), *osmundacea* (28).

VENEZUELA: 6 species, 2 endemics. **serratifolia** (1), *sorbifolia* (5), *caudata* (9), *glandulosa* (12), *osmundacea* (28), **canaliculata** (32).

COLOMBIA: 17 species, 6 endemics. *polybotryoides* (2), *suberecta* (3), *sorbifolia* (5), *crassirhizoma* (7), *caudata* (9), *pubens* (11), *lechleriana* (13), **attenuata** (14), **stolzei** (15), **botryoides** (17), **lourteigiana** (18), **pittieri** (19), *hickeyi* (21), *altescandens* (26), *osmundacea* (28), **latisquamosa** (30), *sessilisora* (31).

ECUADOR: 14 species, 3 endemics. *polybotryoides* (2), *suberecta* (3), **andina** (4), *fractiserialis* (6), *crassirhizoma* (7), *caudata* (9), *pubens* (11), *lechleriana* (13), *alfredii* (16), **puberulenta** (22), *aequatoriana* (24), **appressa** (25), *altescandens* (26), *osmundacea* (28).

PERU: 11 species, no endemics. *polybotryoides* (2), *suberecta* (3), *fractiserialis* (6), *crassirhizoma* (7), *caudata* (9), *pubens* (11), *glandulosa* (12), *lechleriana* (13), *alfredii* (16), *altescandens* (26), *osmundacea* (28).

BOLIVIA: 10 species, no endemics. *fractiserialis* (6), *crassirhizoma* (7), *caudata* (9), *pubens* (11), *lechleriana* (13), *alfredii* (16), *hickeyi* (21), *puberulenta* (22), *aequatoriana* (24), *osmundacea* (28).

PARAGUAY: 1 species, not endemic. *goyazensis* (10).

BRAZIL: 13 species, 5 endemics. *sorbifolia* (5), *crassirhizoma* (7), **espiritosantensis** (8), *caudata* (9), *goyazensis* (10), *pubens* (11), *glandulosa* (12), **cylindrica** (20), *osmundacea* (28), *sessilisora* (31), **semipinnata** (33), **speciosa** (34), **pilosa** (35).

caudata, *P. osmundacea*, and *P. polybotryoides*. As noted in the previous paragraph, *P. caudata* and *P. osmundacea* have the most extensive range of any species in the genus. Although not as wide ranging, *P. polybotryoides* has a long north-south distribution from Chiapas, Mexico, to Pasco, Peru, and is the most far-ranging species of the subgenus *Soromanes*. This distribution supports Tryon's (1970) findings that the ferns of oceanic islands tend to be those that are widespread beyond the source area for the island (the source area for Cocos Island is defined by Tryon as Central America and Colombia). According to Tryon (1970), widely distributed species have a broader ecological amplitude and therefore establish themselves more often on oceanic islands because of their ability to grow under a wide range of environments.

Morphology and Anatomy

Information on the morphology and anatomy of *Polybotrya* has been extremely useful for assessing affinities of related genera and for understanding functional aspects of the biology of the genus. Every phylogenetic argument made here relies heavily on evidence from stem anatomy (along with other features, of course) in determining how *Polybotrya* relates to other fern genera and families. Anatomical studies have also answered other biological questions about the genus. For example, studies of the diplodesmic venation system showed how the sori are efficiently supplied with water and nutrients. Studies of sterile-fertile transitional leaves established that the diplodesmic veins are homologous with the veinlets of the sterile leaves. In short, anatomical studies of root, stem, and leaf have been valuable in understanding diverse questions about the biology of *Polybotrya*.

Roots

A dense tangle of dark, tough, fibrous, adventitious roots arises from the ventral side of climbing stems and from all sides of terrestrial stems. No positional relationship exists between the leaf bases and the roots; roots are apparently borne at random. Roots arising directly from the stem measure about 1 mm in diameter, but their terminal branches may be only 0.3 mm wide. Roots branch at irregular intervals, increasing the number of tiny supportive rootlets. On climbing plants, these tenacious rootlets penetrate the outer layers of tree bark and firmly anchor the stem. This firm attachment hinders pulling the stem away from the tree. When a stem is forcibly pulled away from a trunk, the large roots of *Polybotrya* remain attached to the stem, clinging to shredded pieces of bark, lichens, and mosses.

I studied the root anatomy of six species—*P. alfredii*, *P. caudata*, *P. gomezii*, *P. osmundacea*, *P. polybotryoides*, and *P. sorbifolia*. All were similar. Figure 5a shows

TABLE 4. Affinities of *Polybotrya* floras between regional centers (see Fig. 3). Floristic affinity is the percent species in common (C) of the total species in the two regions (A + B), i.e., 100C/A + B.

Regional Center (Tryon 1972)	Total Species (A + B)	Species in Common (C)	Floristic Affinity (%)
Andean & Guianan	29	5	17.2
Central American & Andean	30	5	16.6
Andean & Southeast Brazilian	28	0	0
Central American & Guianan	13	3	23.0
Guianan & Southeast Brazilian	11	0	0
Central American & Southeast Brazilian	12	0	0

a root in cross section taken about 0.5 cm from the ventral surface of a scandent stem of *P. osmundacea*. The stele is weakly elliptic, protostelic, and comprises about one-fifth of the root's diameter. Two protoxylem poles occur; each is exarch and consists of four to seven protoxylem elements. The center of the stele contains three to five large metaxylem cells. Surrounding the xylem are phloem elements—minute, angular, thin-walled cells about the same diameter as the protoxylem elements. They are not shown in Figure 5a because they were poorly preserved.

Surrounding the stele is the innermost layer of the cortex—the endodermis. It consists of a single, continuous, light-colored layer composed of thin-walled, rectangular

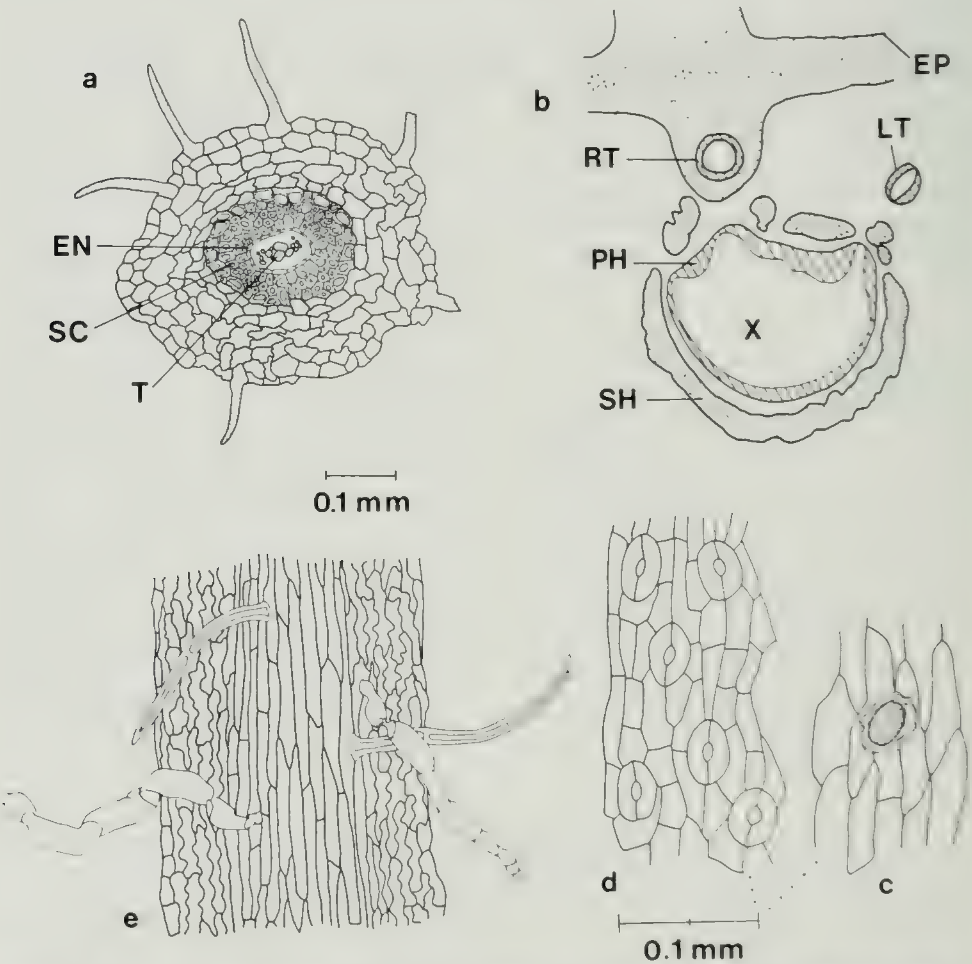

FIGURE 5. Root anatomy and various epidermal features of *Polybotrya*. a,b, and c are the same size. a. root cross section of *P. osmundacea*; b. close-up of a stem meristele in cross section, showing root trace diverging about midway between the laterally diverging leaf traces; c. phloroglucinol-containing gland from the stem epidermis of *P. caudata*; d. stomata on stem aerophore of *P. caudata*; e. fertile segment of *P. stolzei*, adaxial surface. Note different shapes of epidermal cells and the two kinds of hairs; the flaccid hair represents the type that intergrades with scales. EN endodermis; EP epidermis; LT leaf trace; PH phloem; RT root trace; SC sclerenchyma; SH sclerenchyma sheath surrounding a meristele; T tracheid; X xylem.

cells. Although the endodermis is narrow, it contrasts sharply with the dark, thicker-walled cells on either side. The anticlinal walls have casparian strips that are easily visible even in unstained material.

Outside the endodermis is a ring of dark, thick-walled fibers (Fig. 5a). This ring is the most conspicuous feature of *Polybotrya* root anatomy. Unstained, the walls of the fibers appear orangy or reddish and may become so thick that they nearly occlude the entire lumen of the cell. The walls thicken evenly on all sides, unlike many angiosperms and some ferns where the deposition of cell walls occurs centripetally (Bierhorst 1971; Wagner 1952).

Outside the ring of dark fibers, the cortical cells take on a different appearance. In contrast to the cells of the inner ring of fibers, the outer cortical cells are parenchymatous with thin, irregular, dark brown cell walls.

Cells of the epidermis are compact and quadrangular, in contrast to the shape of the cortical cells immediately below. The most conspicuously differentiated cells of the epidermis are the root hairs, generally 0.2–1.0 mm long and straight, narrow, and unicellular. Their color normally varies from brown to amber, but brilliant yellow hairs occur in several species. Unfortunately, the root anatomy of *Polybotrya* cannot be compared with that of other genera of dryopteroid ferns because of inadequate information for those genera.

Stem

Habit. The stem is climbing in all species of *Polybotrya* except for *P. fractiserialis* and *P. sorbifolia*, where it is terrestrial (Fig. 1). Climbing stems grow horizontally about 0.5–2.0 cm beneath the forest floor until they contact a tree. The stem then turns upward, anchoring itself to the tree by adventitious roots produced on the ventral surface. Stems usually climb to a height of 1 to 5 m, but the highest scandent stem I saw was just under 15 m. The longest underground stem that I saw was traced back 8 m from where it entered the soil at the base of its support tree. As a stem begins to climb, it grows wider. The diameter of a climbing stem may reach 3.5 cm; terrestrial stems seldom grow wider than 1 cm. The internode length on climbing stems is generally 10–15 cm.

Stems of the two terrestrial species of *Polybotrya* differ in overall appearance from stems of the climbing species. Stems of terrestrial species are about 15–20 cm long with internodes 1–3 cm long. These short internodes impart a basketlike aspect to the arrangement of leaves instead of the linearly spaced aspect typical of the leaves of climbing species (Fig. 1). The amount of scale cover is another difference. Stems of the terrestrial species are less scaly than stems of climbing species due to the sloughing off or rotting away of scales, presumably because the scales are buried in moist, tropical soils where decay is rapid. Furthermore, the petiole bases hide the few scales that remain in terrestrial species; the best place to find scales is the stem apex, where there is less decay and fewer petiole bases. Despite these differences, both types of stems show affinity by sharing the distinctive anatomy described below.

Branching is rare in stems of *Polybotrya*. I never saw dichotomy of the stem apex, and lateral branching was exceedingly rare in scandent stems, although occasional in terrestrial portions. I did not investigate the relationship, if any, of branching to leaf position, but that examination might provide further evidence for comparisons with other genera of dryopteroid ferns.

Anatomy. The stems of all dryopteroid fern genera have radially symmetric dictyosteles; however, the stems of *Polybotrya* are distinctive (Fig. 6). The most noticeable feature in cross section is the vascular bundles—terete, circularly arranged, each bundle ensheathed by a jet-black ring of sclerenchyma. The 5 to 12 vascular bundles are positioned around the central portion of the stem, their dark outlines contrasting vividly with the matrix of bright white ground parenchyma. Numerous tiny leaf traces emanate from the

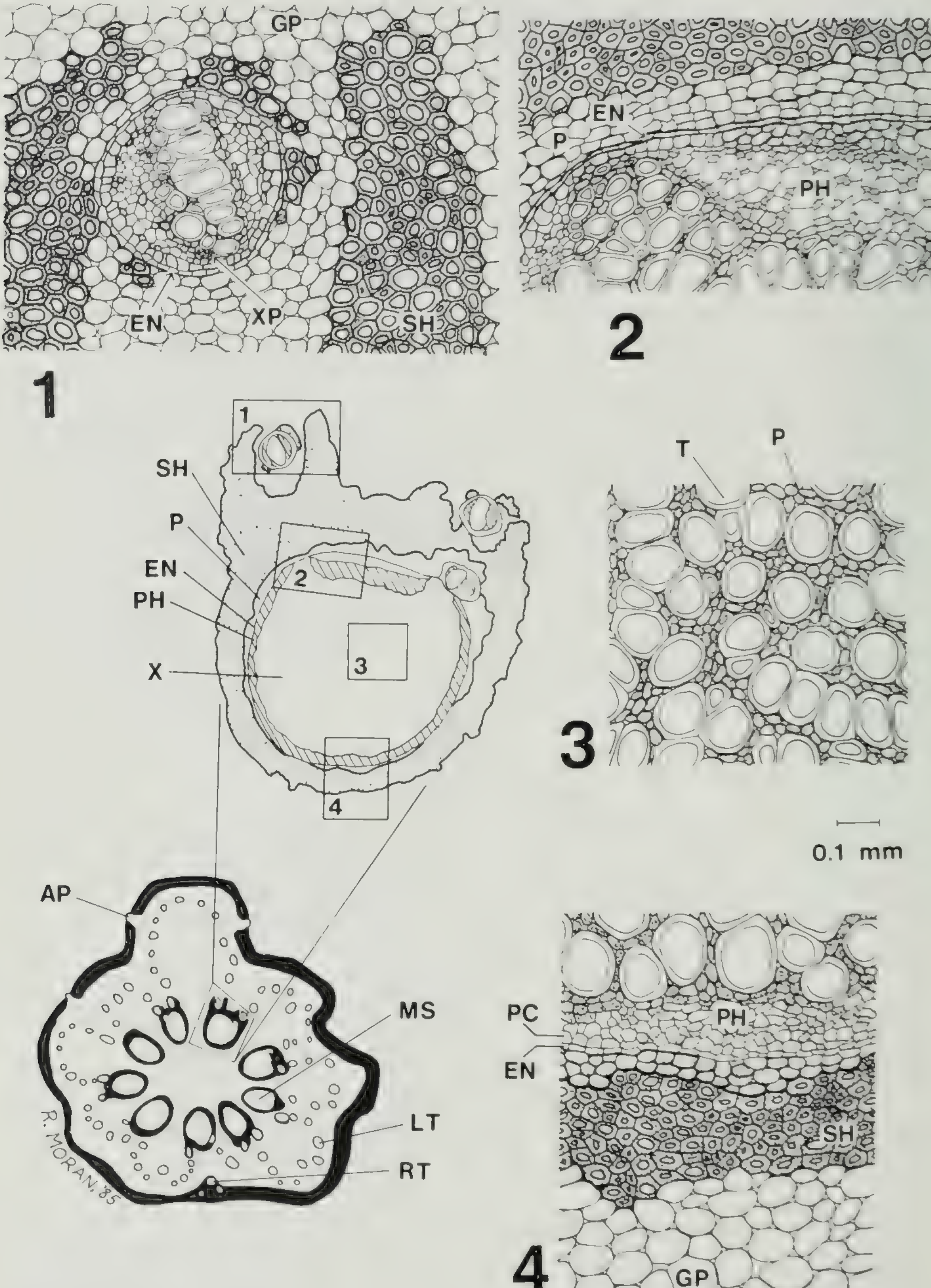

FIGURE 6. Stem anatomy of *Polybotrya osmundacea*, typical of the genus. Lower left is a cross section of the stem with a meristele enlarged above. Note "xylary arm" in 2. AP aerophore; EN endodermis; GP ground parenchyma; LT leaf trace; MS meristele; P parenchyma; PC pericycle; PH phloem; RT root trace; T tracheid; SH sclerenchyma sheath consisting of fibers; X xylem; XP protoxylem.

sides of the bundles, collectively forming a C-shaped line that connects adjacent bundles. This pattern is unmistakable (Fig. 6), and no other fern genus yet studied has this kind of stem anatomy. (For comparison of stem anatomy with closely related groups, see Relationships with Other Groups.)

The epidermis of the stem is darkly sclerotized and one cell layer thick; it produces numerous scales (described separately below). The cell walls of the epidermis are relatively straight compared to the sinuous ones of the leaf epidermis (cf. Figs. 5c & 9).

The stems of *Polybotrya* have minute glandular hairs on the epidermis. These short-stalked hairs have, in relation to their length, exceptionally large, round heads, 54–56 microns in diameter (Fig. 5c). Because these glands are tiny and few, they had been overlooked until found by Widén et al. (1983), who were also the first to report phloroglucinols in *Polybotrya*. The phloroglucinols are apparently produced and stored in these glands. In other dryopteroid ferns, such glands are known to secrete an oleoresin, along with various lipids, between the cuticle and the outer layer of the cell wall. The phloroglucinols are, presumably, located in this secretion (Widén et al. 1983). Using extracts from the stem and petiole bases of *P. caudata*, Widén et al. found that aspidin BB was the principal compound, along with smaller amounts of albaspidin BB, desaspidin BB, and flavaspidic acid BB. Internal glandular hairs, which probably also contain phloroglucinols, occur in the stems and petioles of other dryopteroid ferns (Mehra & Mittal 1961). I did not, however, find internal glands in *Polybotrya*.

Aerophores occur on the stems of most species of *Polybotrya* but are apparently absent in species having a mat of thick, woollike scales, such as in *P. aequatoriana*, *P. altescandens*, and *P. crassirhizoma*. On living stems, aerophores appear as yellowish white lines 1–3 mm wide that connect with aerophores on the petiole (for description of petiolar aerophores, see section below on petioles). Aerophores usually extend 2–6 cm down the stem from the base of the petiole. In cross section, they project about 0.5–1 mm above the surrounding surface and consist of thin-walled parenchyma cells that interrupt the otherwise continuous, thickened epidermis (Figs. 6 & 16g). Stomata abound and can be seen with a binocular microscope (Fig. 5d). Presumably, aerophores allow oxygen into the stem that is otherwise surrounded by compact, oxygen-impermeable, sclerenchyma fibers. Because aerophores shrink and darken upon drying, thereby matching the contour and color of the stem's sclerenchyma, they cannot be seen on herbarium material.

Below the epidermis is a well-developed hypodermis, usually three to eight cells thick and darker than the epidermis that forms a conspicuous ring around the white ground parenchyma. The cells of the hypodermis are thick-walled sclerenchyma fibers that thwart cutting the stem, sometimes even with a hefty machete, and I had problems cutting thin, even, cross sections for microscopic study. A ring of hypodermal sclerenchyma also encircles the stem in closely related genera such as *Arachniodes*, *Cyclodium*, *Maxonia*, *Olfersia*, and *Stigmatopteris* (pers. obs.).

Below the hypodermis lies the cortex, which consists of scattered clusters of brachysclereids (stone cells) in a matrix of whitish parenchyma. The parenchyma cells are generally rounded and contain abundant amyloplasts. In a freshly cut stem, the white color of these cells contrasts vividly with the darkly sclerotized hypodermal and meristelar sheaths. Sclereids never abound, as in *Olfersia* (Fig. 16i), but are scattered in clusters throughout the ground parenchyma. The deposition of secondary walls is extremely uneven; most of the wall is laid down on the side of the cells facing the inside of the sclereid cluster. A small, cuplike lumen can usually be seen on the side of the cell facing away from the center of the sclereid cluster. The thick, dark cell walls contain numerous simple pits and a lesser number of ramiform

pits. Many Dryopteridaceae and Lomariopsidaceae also have sclereid clusters in the ground parenchyma of their stems (pers. obs.).

Inside the sclerenchyma sheath that surrounds each meristele lies a band of parenchyma two to four cells wide (Fig. 6). The cells of this layer are more compact and smaller than the cortical parenchyma, but like the cortical parenchyma, they contain amyloplasts. This inner parenchymatous layer stops abruptly at the endodermis, which stands out as a single row of clear, narrow, rectangular cells interrupting the darker parenchyma on either side of it (Fig. 6). The next layer toward the center is the pericycle, which consists of compact, orangy cells that form a continuous band around the xylem and phloem.

The phloem consists mostly of clear, angular, thin-walled sieve cells (Fig. 6.2 & 6.4). Phloem is broadest on the distal side of the stele but forms a thin band elsewhere. This band is broken in two locations by arms of the xylem that extend to the pericycle (Fig. 6.2). Scattered among the clear cells of the phloem are parenchymatous cells.

Inside the ring of phloem is the xylem, which has large, conspicuous metaxylary tracheids (Fig. 6.3). These tracheids occur singly and in clusters within a matrix of dark brown (when unstained) parenchyma. The tracheids are generally rounded or somewhat angular; when adjacent to another tracheid, the walls are straight. Numerous pits occur between all the cells of the xylem. Protoxylem elements occur in the xylary "arms" (Fig. 6.2). Each meristele is, therefore, diarch and exarch.

Root traces arise between the xylary arms of the meristele (Fig. 5b). The roots diverge through the cortex to the ventral surface of the stem. In contrast to the root traces, the leaf traces originate from the xylary arms. Four to six leaf traces are usually produced at each leaf gap from adjacent meristeles. During their passage from the cortex to the petiole, the leaf traces bifurcate and anastomose, forming a reticulum like that in *Maxonia* (Chandra 1975). Each leaf trace is surrounded by a single layer of sclerotized cells (Fig. 5b). The walls of these cells are brownish and slightly thickened on the inner tangential surface. The distance from the inception of a leaf gap to the point where the leaf diverges from the stem is about 10–15 cm.

Stem scales. Many species of *Polybotrya* have distinctive stem scales. Some species, in fact, can be identified solely on the basis of their stem scales (thus the importance of always collecting part of the stem). Color is the easiest feature of the scales to use in identifying the species of *Polybotrya*. Botanists should have no difficulty identifying *P. altescandens*, with its bright golden or yellow scales; *P. crassirhizoma*, with its dull orange or red scales; and *P. latisquamosa*, with its shiny, castaneous scales. Depending on the species, scales range from concolorous to slightly darker in the center to bicolorous with a dark central stripe.

Scale habit is another helpful identification feature. Some species, such as *P. altescandens* and *P. crassirhizoma*, have narrow, densely tangled scales that impart a woolly appearance to the stem. Other species, such as *P. appressa*, *P. caudata*, and *P. cylindrica*, have thick, dark, massive scales that are conspicuously appressed to the stem. Because of their great width and spreading habit, the scales of *P. serratifolia* are distinct from those of other species of the subgenus *Soromanes*. Most species of *Polybotrya* have ascending and slightly spreading scales—a characteristic that is not particularly distinctive because of its prevalence in the genus.

The shape of stem scales is usually not helpful in identification because most species have lanceolate to linear-lanceolate stem scales. Two species, however, *P. alata* and *P. altescandens* (Figs. 42 & 45), have extremely long, attenuate scales that differ strikingly from those of the other species. Petiole scales are generally similar to those of the stem but tend to be shorter and wider. The petiolar scales of *P. latisquamosa* have become, as the specific epithet implies, greatly widened so that this characteristic distin-

guishes the species from all others in the genus (Fig. 50d).

Despite variation in color, habit, and shape, stem scales are of two general types, here termed simply Type 1 and Type 2. Scales of Type 1 are thin and translucent and have easily visible cell walls (Fig. 7). Most of the scale is one cell layer thick, although the center may be thicker and darker. The margins vary from denticulate to erose, with the teeth formed from the projecting ends of two adjacent cells (Fig. 7). Marginal teeth in

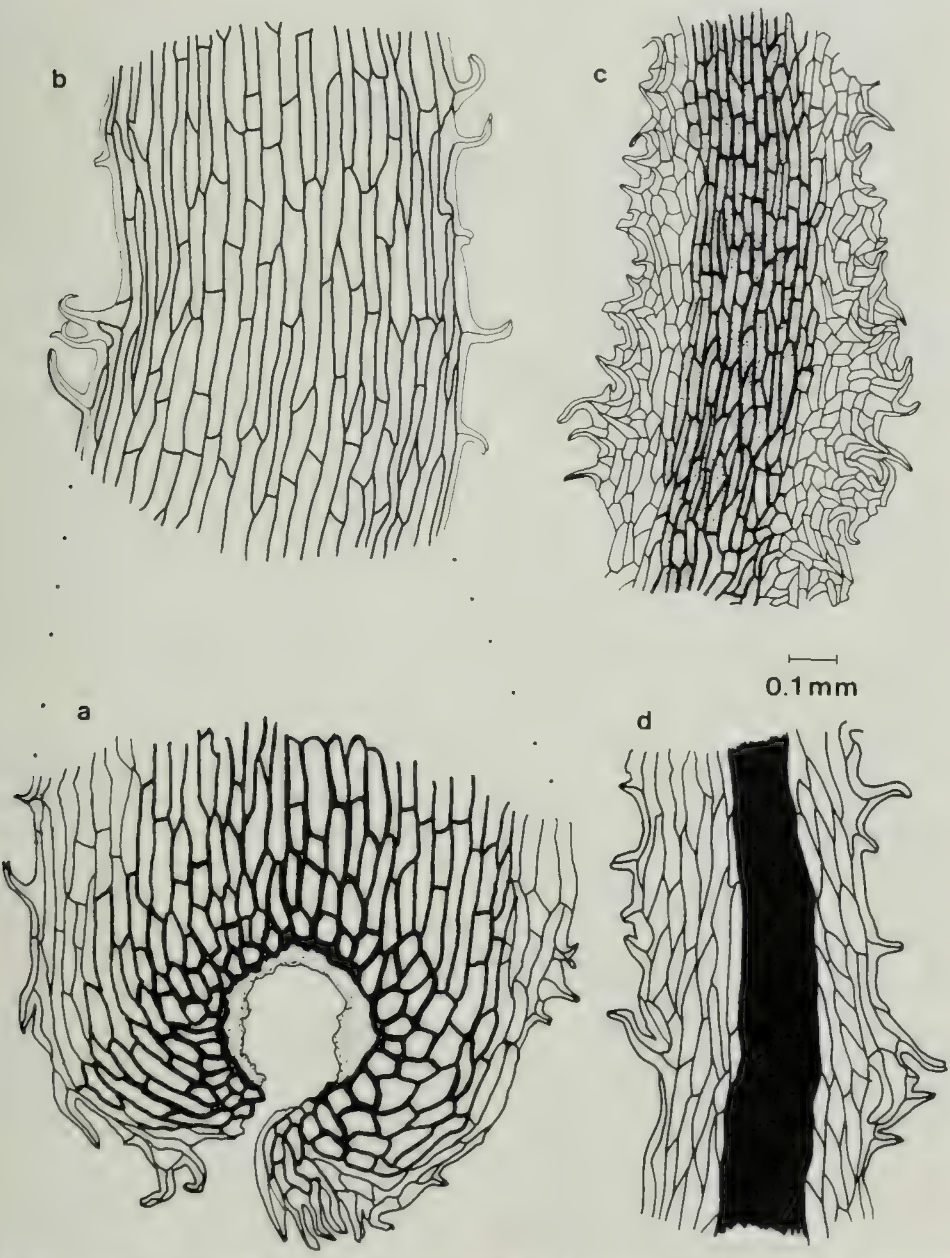

FIGURE 7. Stem scales of various *Polybotrya* species. a, b. *P. altescandens*; c. *P. botryoides*; d. *P. crassirhizoma*.

Polybotrya are never glandular, as in *Bolbitis* (Hennipman 1977) and *Stigmatopteris* (pers. obs.). Scales of Type 1 are attached basally at a single point or, more rarely, across the full length of the base. This point or line of attachment is always darkly sclerotized (Fig. 7a). Representative species with scales of Type 1 include *P. crassirhizoma*, *P. goyazensis*, *P. puberulenta*, and *P. serratifolia* (Figs. 26, 29, 41, & 19).

Scales classified as Type 2 are thick, opaque, and composed of many cell layers. The margins are entire or subentire. The base is greatly thickened, sometimes almost stipelike, and is curved and ascending. When the scale is removed, a circular or oval scar remains on the stem. Scales of this type are usually appressed, but they are squarrose in *P. osmundacea*. Representative species with scales of Type 2 include *P. appressa*, *P. caudata*, and *P. cylindrica* (Figs. 44, 28, & 39). In contrast to scales of Type 1, which show tremendous variety in habit, color, and shape, those of Type 2 are relatively homogeneous.

Evidence suggests that morphological transition occurs easily between the two types of scales. Species such as *P. lechleriana*, *P. lourteigiana*, *P. osmundacea*, and *P. pubens* have both types of scales but on different individuals. Even on a single plant, scales belonging to Type 1 can occur on the climbing portion, with scales of Type 2 and/or intermediates on the terrestrial portion. If morphological transition is easily accomplished, then evolutionary change in scale type could be expected to occur in closely related species pairs. This hypothesis is supported by two closely related species *P. caudata* and *P. goyazensis* (Figs. 28 & 29); the former has scales of Type 2 whereas the latter has scales of Type 1. Clearly, the stem scales of *Polybotrya* have been morphologically and evolutionarily plastic.

The evolutionary advantage of scales in *Polybotrya* is unknown. Their contribution to protecting the stem from mechanical damage is probably minimal since the stem is surrounded by a tough, resistant, sclerenchymatous sheath. Scales seem unnecessary on the older, hardened parts of the stem. During fieldwork in Latin America, I found several plants of *Polybotrya* that had lost all of their scales on the lower, older part of the climbing stem, yet the plants appeared vigorous. Perhaps the scales afford protection to the stem apex, where young tissues have not yet become sclerified.

Another hypothesis is that the scales retain water by capillary action for later use by the roots. Retention would be advantageous to a climbing plant that has the leaves on the scandent portion of the stem separated by several meters from the roots in the soil. Stems collected in the field, however, never seemed to hold water between the scales and plants never appeared water stressed. The bark of the support tree, which is usually covered with water-retaining mosses, lichens, and organic debris, probably could provide most of the water needed by the plant. Further, the retention of capillary water between stem scales might be harmful in a hot, humid, tropical environment that promotes decay. No satisfactory hypothesis, therefore, has been offered to explain the adaptive significance of scales in *Polybotrya*.

Even more difficult to explain is the adaptive advantages of the numerous minor modifications of scales. What could be the function of a dark, central stripe, of reddish color, of an appressed habit, or of a linear shape? How these and other minor modifications of scales are significant in evolution, if indeed they are, is baffling.

Leaves

Petiole. The petiole base in some ferns is specialized to accumulate food and to persist as a storage organ long after the rest of the leaf to which it was attached has withered and decayed. These specialized petiole bases, called "trophopods," are a new source of systematic data in ferns (Wagner & Johnson 1983). *Polybotrya*, however, lacks trophopods, and the food-storing function of the trophopod is performed by the stem in the

amyloplast-containing cells of its ground parenchyma.

A cross section of the petiole of *Polybotrya* reveals leaf traces that are arranged in a mushroomlike outline, with the base of the mushroom oriented adaxially (Fig. 8a). This pattern also occurs in *Cyclodium trianae*, a species closely related to *Polybotrya*, and in some species of the similar family Lomariopsidaceae (Hennipman 1977; Holttum 1978). Other closely related dryopteroid genera, however, such as *Cyrtomium*, *Dryopteris*, and *Polystichum*, display a C-shaped arrangement of leaf traces in the petiole (pers. obs.). These genera also have fewer leaf traces than *Polybotrya*, probably as a consequence of their narrower petioles. Further study of petiole anatomy in dryopteroid genera may provide helpful information for assessing their relationships.

In *Polybotrya*, the two vascular bundles closest to the adaxial surface of the petiole differ from the lower vascular bundles in several respects. The most obvious difference is their shape: elongate and slightly curved instead of round (cf. Fig. 8b,d). Inside each of the two adaxial bundles, the xylem is hook-shaped in outline, in contrast to the lenticular shape seen in the lower traces. Only these uppermost vascular bundles, not the lower, yield the lateral traces that supply the pinnae. As they traverse the rhachis and petiole, all traces remain separate; they do not anastomose to form a reticulum within the petiole.

Aerophores run down the sides of the petiole and join below with those on the stem. On living petioles, they appear narrow, linear, and light green. The surface of the aerophores bears stomata, and beneath them is parenchyma that contains intercellular spaces. This parenchyma, when seen in cross section (Fig. 8c), interrupts the otherwise continuous band of collenchyma that encircles the petiole. Upon drying, the aerophores darken and collapse, leaving a sulcus on either side of the central, adaxial sulcus of the petiole. Drying, therefore, makes the petiole trisulcate; in living petioles only a central sulcus is present.

Petiole and stem mucilage. Mucilage has apparently never been reported in *Polybotrya* or any other genus of Dryopteridaceae. During fieldwork in Costa Rica and Ecuador, however, I found that stems and petiole bases of *P. alfredii* usually had a thick coat of translucent mucilage similar to that on the stems and/or petioles of certain *Blechnum* and *Thelypteris* species. Upon drying, the mucilage disappeared completely, although sometimes the scales exhibited a matted or flattened appearance, as if stuck together. Attempts to rehydrate the mucilage failed.

Other species of *Polybotrya* probably have mucilage. Several dried specimens of *P. lechleriana* and *P. lourteigiana* exhibited matted, flattened scales that suggested the earlier presence of mucilage. These two species are closely related to *P. alfredii*, an observation that suggests that mucilage is probably confined to the *P. alfredii* group (species nos. 13–20). I did not see matted, flattened scales in any other species of *Polybotrya*. The mechanism of mucilage secretion and its adaptive significance, if any, is unknown.

Nectaries. Koptur et al. (1982) were the first to report the existence of nectaries in *Polybotrya*. They found them in *P. osmundacea* on the rhachis of unfurling leaves, near the yellowish, lateral, linear aerophores. Several times during fieldwork in Costa Rica, I noticed ants on young leaves, but I never saw them feeding on nectar. The nectar itself would certainly be nutritious because it contains sucrose, glucose, and fructose in concentrations up to 35–75 percent by weight (Koptur et al. 1982). Amino acids also occur in the nectar, and Koptur et al. list those present. Although ants may benefit from the nectaries, additional fieldwork is needed to establish whether or not the plants benefit. Apparently, ants do not defend the plants—at least I was never attacked by ants while collecting *Polybotrya*.

Costa-costule architecture. Costa-costule architecture refers to the morphology of the juncture of these axes. Several kinds of

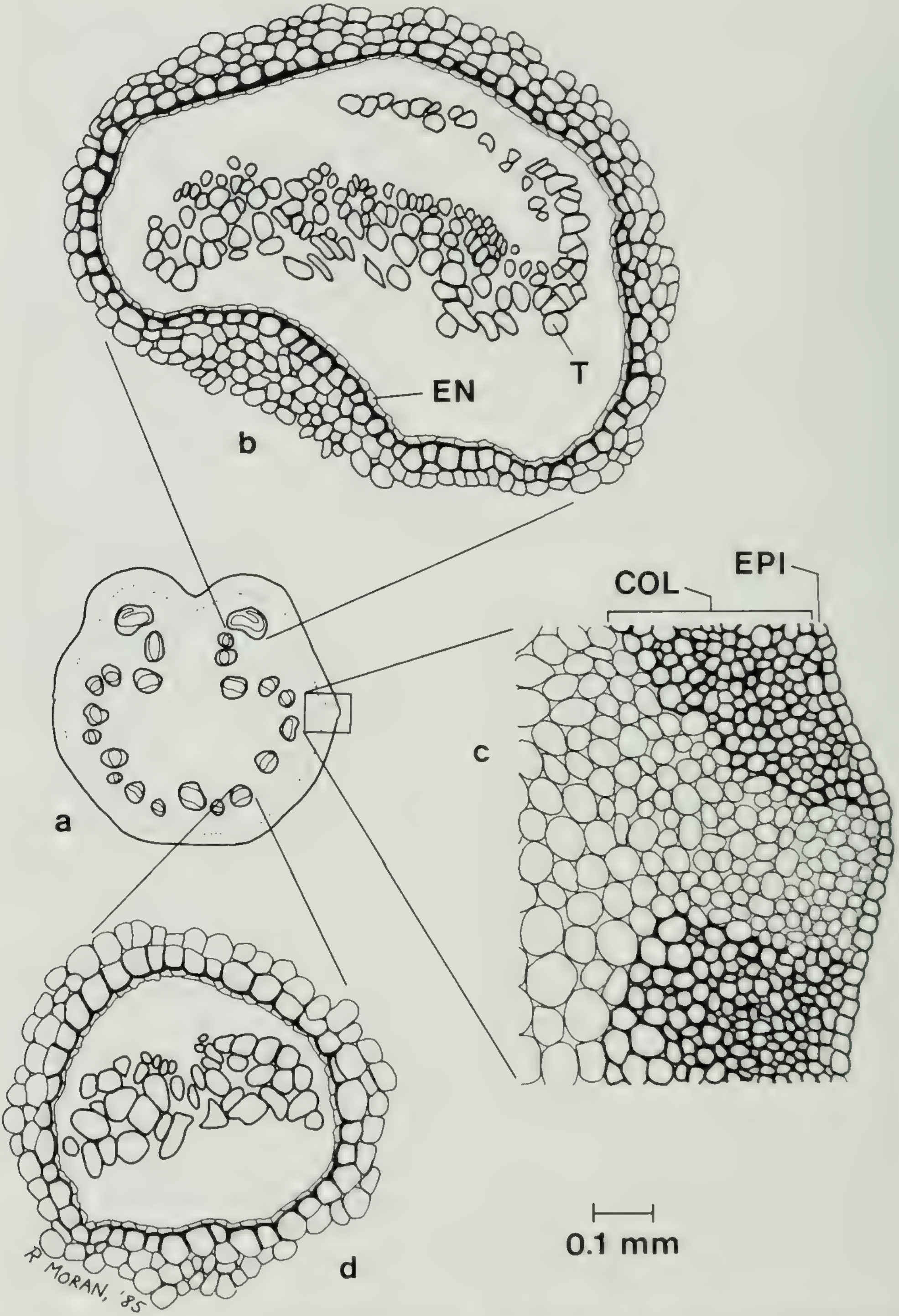

FIGURE 8. Petiole anatomy of *Polybotrya alfredii*. a. cross section of petiole 2 cm above the stem showing the arrangement of vascular bundles in the shape of a mushroom; b. adaxial bundle showing hooked xylem; c. aerophore; d. abaxial bundle. COL collenchyma; EN endodermis; EPI epidermis; T tracheid.

costa-costule architecture occur; the most thorough review of them is by Holttum (1959); more than any other pteridologist, he has shown the importance of this feature in the taxonomy of ferns. According to Holttum (1984), the dryopteroid genera have "midribs of ultimate leaflets grooved, the groove of the rachis bearing the leaflets being open to admit the leaflet-groove, the margin of the lamina of the leaflet being decurrent (but not prominent) down the side of the rachis; hairs of ctenitoid type lacking." This type of architecture is illustrated in Figure 47h. Holttum (1984) describes the tectarioid genera as having "midribs of ultimate leaflets more or less prominent (in *Tectaria* sometimes slightly grooved) and bearing ctenitoid hairs, usually many." In *Polybotrya*, the basic type of architecture is dryopteroid, a finding that supports its classification among the dryopteroid ferns.

Within *Polybotrya*, however, modifications are found in the dryopteroid pattern of costa-costule architecture. Typical dryopteroid costa-costule architecture is shown in the most primitive group in the genus—the group of species related to *P. osmundacea*. In contrast, the most advanced species in the genus—*P. attenuata*, *P. lechleriana*, and *P. stolzei*—always have the costular groove truncated by the ridges of the costa; therefore, the groove is not decurrent (Figs. 33b, 32b, & 34f). This truncated costa-costule architecture is considered to have been derived from the decurrent-grooved condition, as evidenced from outgroup comparison with other dryopteroid ferns. Intermediates, such as *P. aequatoriana* and *P. alfredii*, have costular grooves that gradually fill up near the costa, so that the ridges of the costa are only slightly interrupted by the shallow, weakly decurrent groove of the costule (Fig. 43d). In *P. alfredii* and *P. lourteigiana*, these three types of costa-costule architecture can be found on different parts of the same leaf, although the intermediate type predominates. In summary, most species of *Polybotrya* have dryopteroid costa-costule architecture, but distinctive modifications of this basic type occur.

Anatomy of the lamina. I studied leaf clearings and cross sections for 17 species of *Polybotrya* to determine differences between species or subgenera. Leaf clearings revealed that stomata were absent from the adaxial epidermis but abundant on the abaxial surface between the veins. The long axes of the stomata ran almost parallel to the veins. The mean length of the stomata (for all species) was 56 microns, but means for the species ranged from 48 to 74 microns. Subsidiary cells surrounded the distal one-half to two-thirds of the guard cells. The shape of the subsidiary cells can be like the sinuous epidermal cells or slightly more rounded and circular (Fig. 9d,f).

In face view, the epidermal cell walls fit together like the pieces of a jigsaw puzzle (Fig. 9). This interlocking is best exemplified by the abaxial epidermal cells, which have a more highly irregular outline than the adaxial ones. The cells above and below the veins, however, have straight walls. The slightly elongate axes of the cells are oriented parallel to the veins and point in the direction of the leaf margin.

In cross section, the abaxial epidermis and adaxial epidermis form a single, compact layer of relatively thick-walled cells (Fig. 9g,h). Palisade parenchyma is absent from the mesophyll, which is composed mostly of large intercellular air spaces surrounded by long, cylindrical, parenchymatous cells. An arm of collenchyma extends from the abaxial epidermis to the vein, where it forms a sheath around the vein but does not continue to the adaxial side of the leaf. Leaf anatomy was similar in all species of *Polybotrya*, probably because the entire genus occupies a similar habitat.

Hair types. Two fundamentally different types of hairs occur in *Polybotrya*. One type intergrades with scales, the other does not. The nonintergrading type is erect or spreading, usually cylindrical, and whitish or tawny. The size of hairs of this type varies tremendously, from unicellular hairs that are less than 0.1 mm long and not visible to the naked eye to readily visible acicular hairs

that have up to 15 cells and are up to 2 mm long (Fig. 10 a–i,k). The apical cell is pointed, rarely rounded. All but five species of *Polybotrya* have this kind of hair.

Hair of the second type is fundamentally different from hair of the first type because each hair is a tiny, uniseriate scale and, therefore, by definition, a hair. Every intermediate stage exists between these hairs and the scales, as evidenced by studying their change in form from the apex to the base of the costa (Figs. 10j & 36a,b). At the apex of the costa,

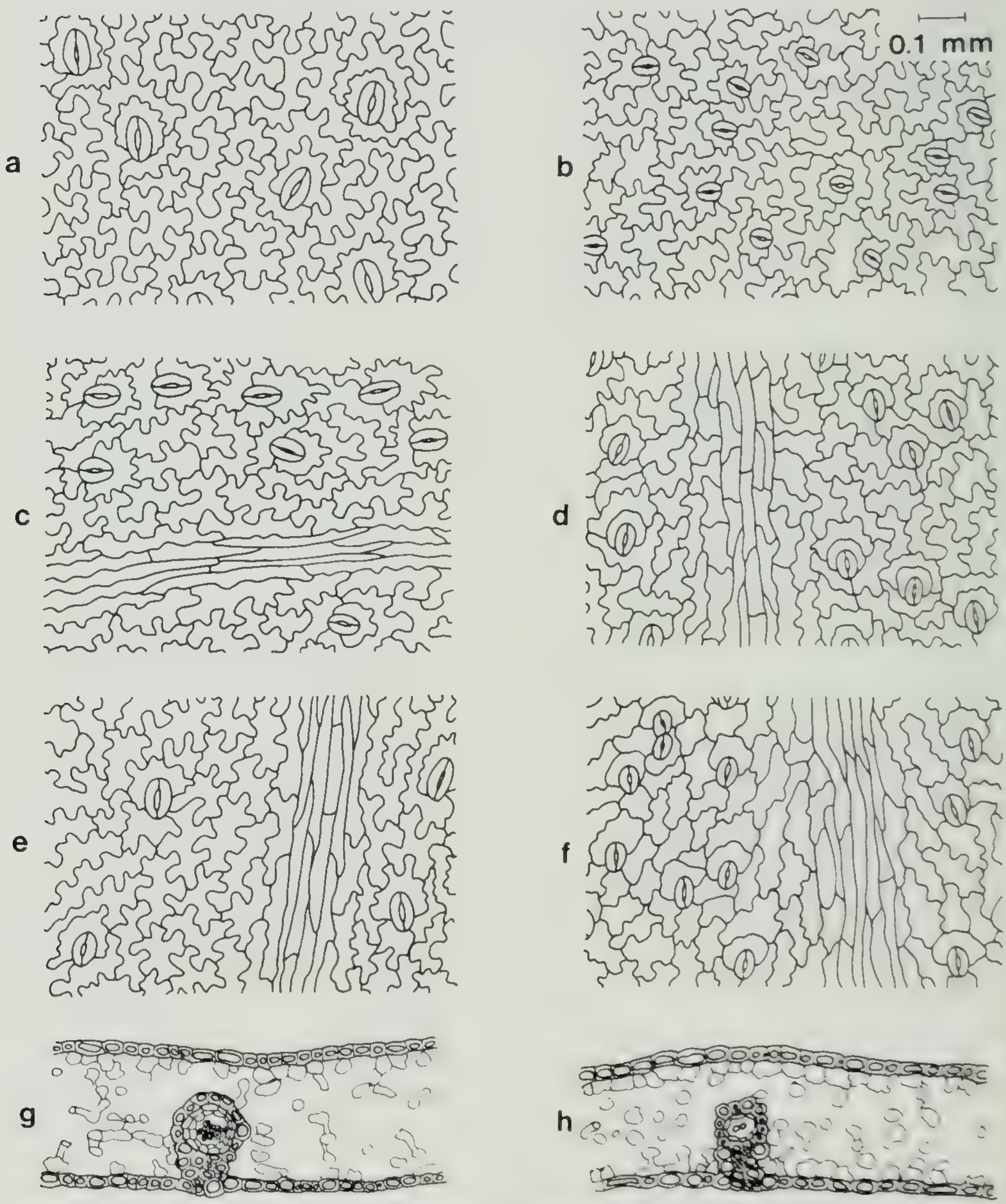

FIGURE 9. Leaf anatomy of *Polybotrya*. a–f. face views of the abaxial leaf epidermis. The elongated cells with straight walls lie above the veins. g, h. cross sections of the leaf. a. *Polybotrya serratifolia*; b. *P. pubens*; c. *P. fractiserialis*; d. *P. canaliculata*; e, g. *P. crassirhizoma*; f, h. *P. speciosa*.

only the tiny uniseriate scales, the "hairs," occur. These are readily distinguished from other hairs by their flattened cells, appressed habit, and darkened transverse walls. Towards the base of the costa, the hairs become longer and are composed of more cells; soon are found "hairs" that are two cells wide near their base, that is, scales. These small scales grade imperceptibly into the larger scales on the rhachis. The scales on the rhachis and costae are, therefore, developmentally homologous with this second kind of hair.

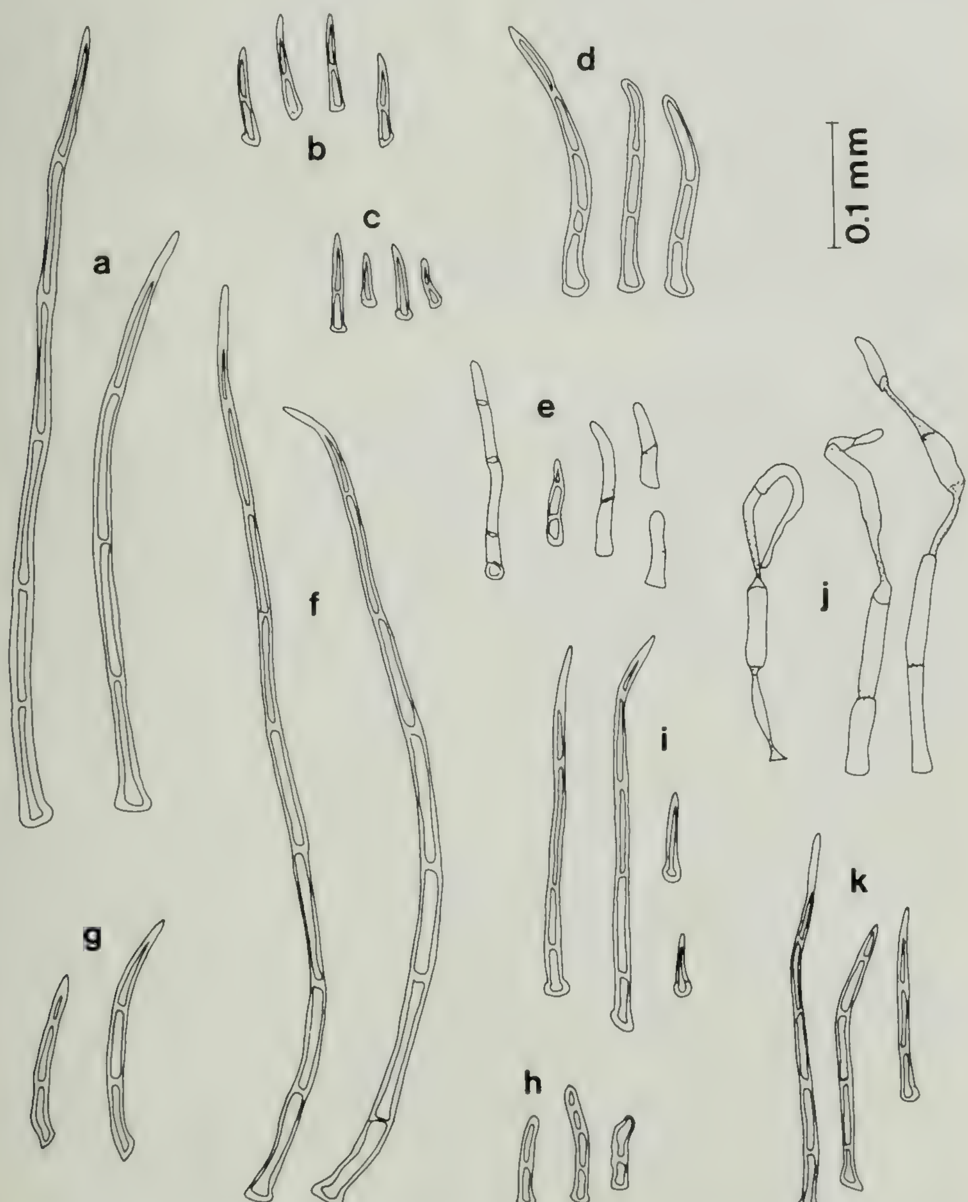

FIGURE 10. Hair types in *Polybotrya* taken from the abaxial surface of the costa. a. *P. pubens*; b. *P. semipinnata*; c. *P. altescandens*; d. *P. pittieri*; e. *P. alfredii*; f. *P. glandulosa*; g. *P. speciosa*; h. *P. osmundacea*; i. *P. caudata*; j. *P. lechleriana* (reduced scale type); k. *P. cylindrica*.

These hairs are called proscales since they are developmentally, and probably evolutionarily, precursors to scales (Moran 1986).

Proscales occur on the lamina and axes of all species of *Polybotrya* and all genera of dryopteroid ferns. Proscales are, however, so minute that pteridologists often overlook them or do not bother to mention them. Proscales are smallest on the distal parts of the lamina (Fig. 49h) and at least 30× is needed to see them. Their flattened cells, often having reddish cross walls, occasionally twist upon drying, imparting the appearance of a *Ctenitis*-hair. These are not true *Ctenitis*-hairs, however, because such hairs never intergrade with scales (Christensen 1913). This nonintergrading feature is rarely mentioned in the definition of *Ctenitis*-hairs.

Fertile Leaves

Moran (1987) has presented a detailed study of the sterile and fertile leaves (trophophylls and sporophylls) of *Polybotrya*. Below is a synopsis of the subject.

The fertile leaves of *Polybotrya* resemble a skeleton of the sterile ones because their green lamina has been reduced to a narrow wing above the veins. This extreme dimorphy, termed "holodimorphy," is distinguished from other types of dimorphy by the nearly total loss of photosynthesis in the fertile leaf (Wagner & Wagner 1977). The reduction of green tissue is the most conspicuous aspect of dimorphy, but differences in seasonality, duration, orientation, insertion on the stem, size, color, texture, and venation are also involved. Thus, sterile-fertile leaf dimorphy is an ensemble of characteristics and not merely a single feature of the leaf. Pteridologists previously described the sori of *Polybotrya* as acrostichoid, but three types of sori occur in the genus: botryoid, coenosoric, and a new type here termed "amphiacrostichoid." Botryoid sori, which are round and discrete, are considered primitive on the basis of outgroup comparison with other dryopteroid ferns (Fig. 38b). The coenosoric type, which are oblong to linear, probably evolved from the botryoid type by basipetal fusion of the sori (Fig. 35h). The amphiacrostichoid type developed from a coenosoric ancestor by the expansion of the margins of the receptacle beyond the original adaxial surface; as a result, the receptacle assumed its own adaxial surface and sporangia appeared on both surfaces of the leaf (Fig. 30g). Coenosoric and amphiacrostichoid sori contain diplodesmic veins that are developmentally homologous with veins of the sterile leaf.

Sporangia. The sporangial stalk of *Polybotrya* is three-celled at its apex, immediately below the capsule. Below the apex, however, only two rows of cells occur, each three to four (rarely 5) cells long (Fig. 11). Where the two rows of the base join the three cells at the apex, a paraphysis occurs; it is always uniseriate, unbranched, and multicellular. About three-fourths of the species of *Polybotrya* have paraphysate sporangial stalks, but paraphyses occur on only 40–80 percent of the stalks from a single sample. In dried or rehydrated material, the apical cell of the paraphysis is smaller and shriveled compared to the cells below. In fresh material, the apical cell appears swollen and glandular. Sporangial stalks of *P. fractiserialis* are unique because they have lightbulb-shaped, glandular cells at the base of the paraphyses (Fig. 11g). The functions of these glandular cells and paraphyses are unknown.

Sporangial capsules of *Polybotrya* are typical of those found in related dryopteroid ferns. The mean number of annular cells for species of *Polybotrya* ranges from 12 to 24, with most species having between 14 and 18. Both the epistomium and hypostomium consist of three or four thin-walled, transversely elongated cells. All species of *Polybotrya* have glabrous sporangial capsules, except *P. pubens*, which has short, subulate hairs at the top of the capsule near the annulus (Fig. 30e,f). Usually two of these hairs occur on either side of the annulus, creating the impression that the capsule has "horns."

Spores. Spore sizes, measured by the longest axis, are given (when available) at the end of each species description. Numbers

are for spores measured immediately after being placed in distilled water because this medium is readily available to taxonomists. Fifteen spores were measured per specimen.

Spores of most *Polybotrya* species range from 45–65 microns in length, with extremes of 32 and 80 microns. According to Tryon and Tryon (1982), *Polybotrya* has relatively large spores compared to those of other genera in their tribe Dryopteroideae. The spores appear dark brown when viewed with transmitted light under a compound microscope but deep orange when viewed with reflected light under a dissecting microscope.

Spores of *Polybotrya* are fairly uniform within the genus compared to the variation encountered in other genera of dryopteroid ferns (e.g., *Dryopteris* and *Polystichum*). *Polybotrya* spores are monolete, with the aperture linear and one-third to three-fourths the length of the long axis. The aperture is often obscured by the broad perispore folds and smaller spines. The exospore appears smooth (Fig. 12), as it does in spores of most genera of dryopteroid ferns. The perispore consists of two layers: the lower layer is thin and appressed to the exospore; the upper layer is thicker, with inflated folds and echinate to various degrees (Fig. 12). No constant differences were found between the three subgenera or smaller species groups.

The principal differences between species appear in the prominence and density of perisporal folds and spines. Typically, the in-

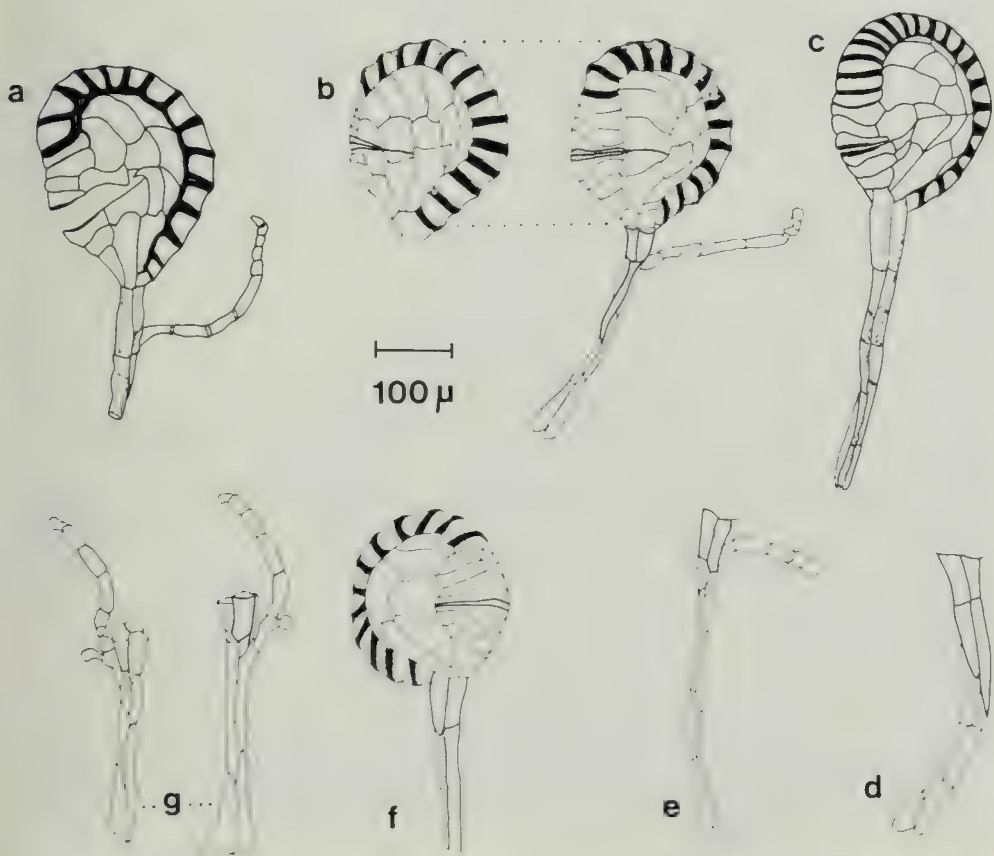

FIGURE 11. Sporangia of various *Polybotrya* species. a. *P. attenuata*; b. *P. sorbifolia*, showing both sides of the same sporangium; c. *P. espiritosantensis*; d. *P. speciosa*; e. *P. osmundacea*; f.g. *P. fractiserialis* (note in g the globose, glandular cell at the base of the paraphysis).

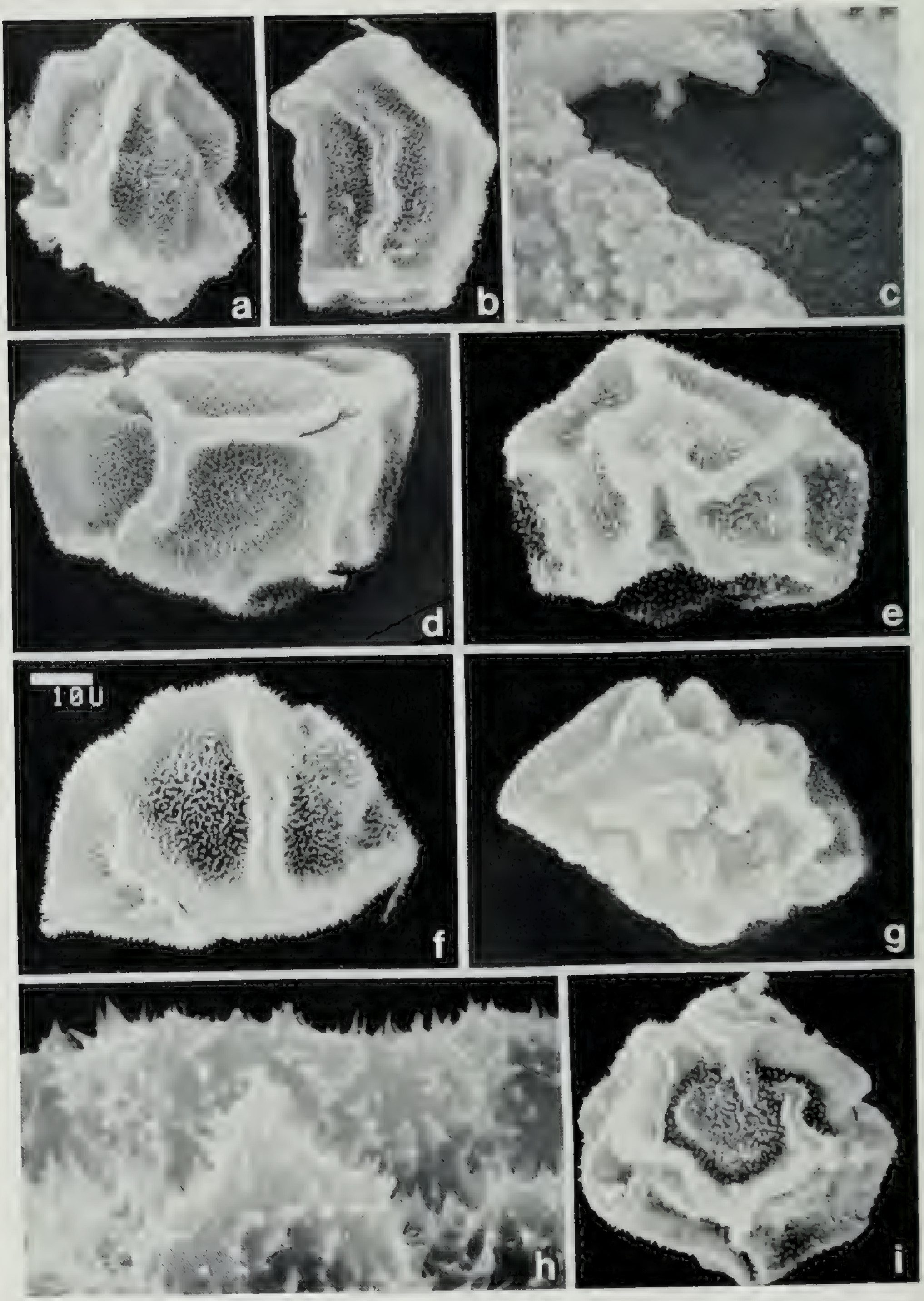

FIGURE 12. Spores of *Polybotrya*. a. *P. semipinnata*; b. *P. osmundacea*; c. *P. serratifolia*; d. *P. pittieri*; e. *P. gomezii*; f. *P. alfredii*; g. *P. crassirhizoma*; h. *P. cylindrica*; i. *P. speciosa*. a: *Duarte et al. 65322* (F). b: *C. Schunke 380* (GH). c: *Fendler 261* (GH). d: *Lellinger & de la Sota 251* (US). e: *Moran 3241* (CR). f: *Moran 3168* (CR). g: *Plowman et al. 4025* (GH). h: *Handro 2228* (GH). i: *Webb 26* (GH). c and h are ×5000, all others are ×1000.

flated folds are well developed and the spines are so numerous that they impart a "fuzzy" appearance. However, the folds may be relatively low, as in *P. goyazensis* and *P. sorbifolia*, or the spines may be reduced in height and/or density, as in *P. speciosa* (Fig. 12i). Species may also differ in spore size. This range is clearly shown by the two terrestrial species in the subgenus *Sorbifolia: P. sorbifolia* and *P. fractiserialis* differ greatly in spore size (40–47 and 52–56 microns long, respectively), a difference that probably reflects different ploidy levels.

Comparison of the spores shown in Figure 12 with the spores of other dryopteroid ferns illustrated by Tryon and Tryon (1982) shows that the spores of *Polybotrya* are most like those of *Maxonia* and *Stigmatopteris* (Tryon and Tryon include *Cyclodium* in *Stigmatopteris*). *Cyclodium*, which is most closely related to *Polybotrya*, has spores similar to those of *Polybotrya* but less spiny (A.R. Smith 1986). This observation supports evidence from external morphology that these genera form a closely related group.

Chromosome Numbers

The only previous reports of chromosome numbers in *Polybotrya* came from two separate counts of *P. osmundacea*, one from Jamaica and the other from Trinidad; both gave a chromosome number of $n=41$ (Walker 1966; Smith & Mickel 1977). To add to the information about chromosome numbers in the genus, I collected meiotic material during fieldwork in Latin America. Young fertile segments were placed for 3–5 hours in distilled water saturated with paradichlorobenzene. The segments were then removed, blotted gently, and placed in a fixative of 3:1 ethyl alcohol to glacial acetic acid. The material was stored in a freezer until it could be examined. Sporangia were squashed in a drop of aceto-carmine and then photographed.

This work recorded new chromosome number counts for four species—*P. alfredii*, *P. altescandens*, *P. polybotryoides*, and *P. serratifolia* (Fig. 13). Each of the four counts had a chromosome number of $n=41$, a finding that argues, along with morphological features, for classifying *Polybotrya* among the dryopteroid ferns, all of which have $n=41$. Chromosome counts are still needed from the other species of *Polybotrya*, especially where polyploidy may be involved in the evolution of one species from another, as in *P. fractiserialis* and *P. sorbifolia*.

Cladistic Analysis of the Species

A cladogram of species relationships was constructed using the PAUP program, version 2.3 (Swofford 1985; PAUP is an acronym for Phylogenetic Analysis Using Parsimony). Table 5 shows the input data used in the analysis, and Table 6 gives the characters and character states used in the input data matrix. The character state trees (hypothesized evolutionary pathways) for the characters (Table 6) are shown in Figure 14. Further information on the characters and justification of their postulated evolutionary pathways is given in the Morphology and Anatomy section.

Because of homoplasy in the data set, PAUP found a large number of equally parsimonious cladograms. Therefore, a consensus cladogram (Fig. 15) was printed for the first 50 trees to determine the branching patterns they all had in common. The 50 trees agreed on the branching patterns for 12 species—about one-third of the genus. The groups that had congruent branching patterns were subgenera *Soromanes* and *Sorbifolia* (Fig. 15, *serratifolia—espiritosantensis*) and the group of species related to *P. caudata* (Fig. 15, *caudata—pubens*). Homoplasy in the remaining species accounted for the numerous, equally parsimonious cladograms. Nevertheless, distinct groups of species are shown on the consensus cladogram, a result that supports the following subdivision of the genus.

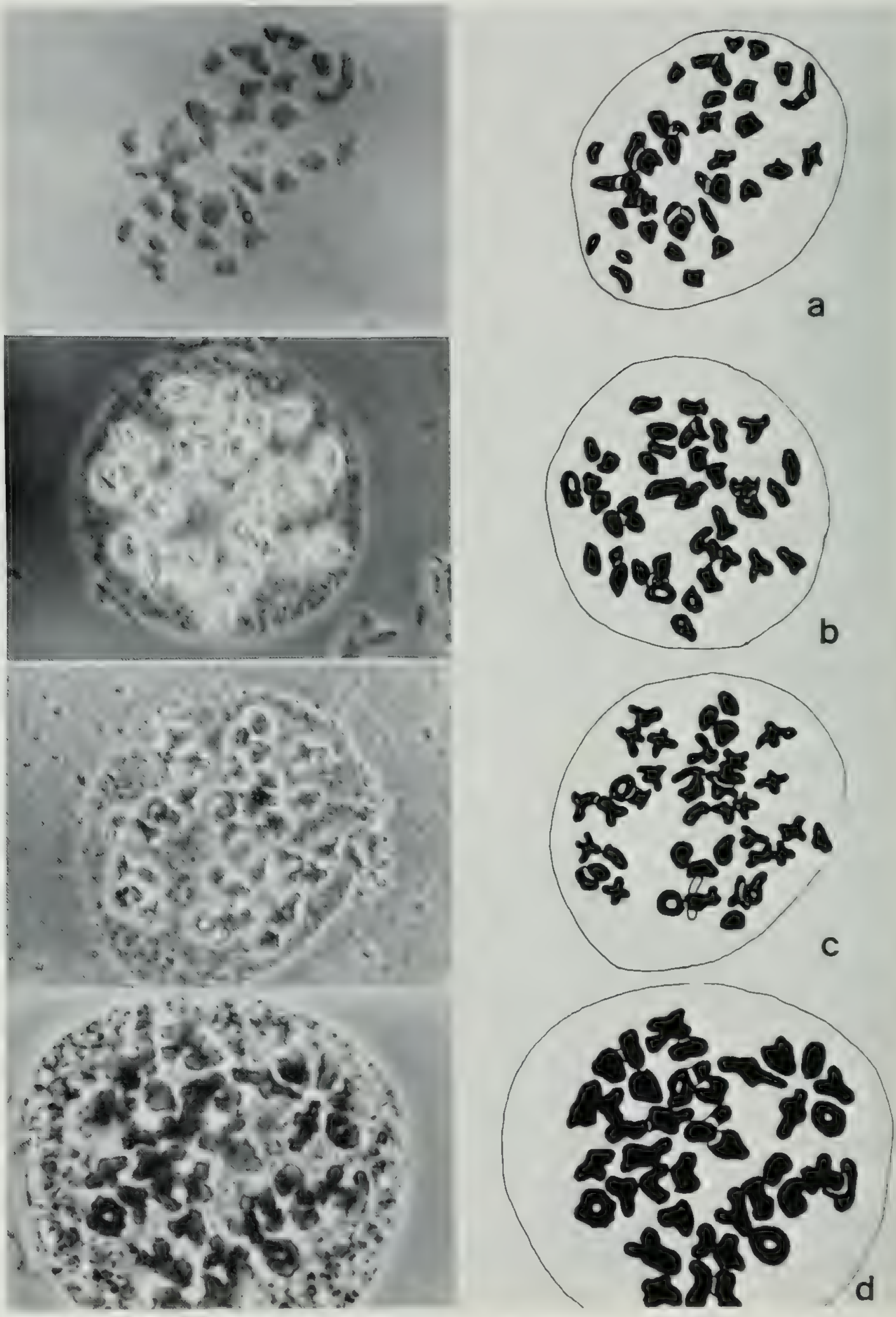

FIGURE 13. Chromosome squashes of four species of *Polybotrya*. All squashes have $n = 41$. My interpretations are at the right. a. *P. altescandens*, Ecuador, Pichincha, *Moran 3559* (GH); b. *P. polybotryoides*, Costa Rica, Cartago, *Moran 2178* (MO); c. *P. serratifolia*, Venezuela, Trujillo, *Moran 3709* (MO); d. *P. alfredii*, Costa Rica, Cartago, *Moran 2442* (CR).

TABLE 5. Data matrix for cladistic analysis of 35 species of *Polybotrya*. See text for discussion of character states and polarity. Ancestor – hypothetical ancestor possessing all primitive character states. ? = unknown character state. NA = not applicable.

	Character States																			
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
serratifolia	5	2	3	0	NA	0	0	1	1	0	2	1	1	0	0	1	0	0	0	0
polybotryoides	5	2	3	0	NA	2	0	1	1	0	2	1	1	0	0	1	1	0	0	0
suberecta	5	2	3	0	NA	1	0	2	2	0	0	1	1	0	0	1	0	0	0	0
andina	5	2	3	0	NA	1	0	1	2	0	0	1	1	0	1	1	0	0	0	0
sorbifolia	5	0	3	0	NA	0	0	1	1	0	2	1	1	0	0	1	0	1	0	0
fractiserialis	5	0	3	0	NA	0	0	1	1	0	2	1	1	0	0	1	0	1	0	1
crassirhizoma	5	0	3	0	NA	0	0	1	1	0	2	1	2	0	0	1	0	0	0	0
espiritosantensis	4	0	4	0	2	0	0	1	1	0	2	1	2	0	0	3	1	0	0	0
caudata	3	1	4	1	1	0	1	0	2	1	0	1	1	0	0	1	0	0	0	0
goyazensis	3	1	4	1	1	0	0	0	2	1	0	1	2	0	0	1	0	0	0	0
pubens	3	1	4	1	1	0	0	0	0	1	0	1	3	0	0	1	0	0	0	0
glandulosa	3	1	2	1	1	0	1	0	0	1	0	2	1	0	0	1	0	0	0	0
lechleriana	0	1	2	1	0	0	?	1	0	0	0	1	3	0	1	0	0	0	1	0
attenuata	2	1	2	1	0	0	0	1	1	0	0	0	1	0	1	2	0	0	2	0
stolzei	2	1	?	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0
alfredii	1	1	3	1	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0
botryoides	0	1	2	1	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0
lourteigiana	3	1	3	1	0	0	?	1	1	0	0	1	1	0	0	0	0	0	0	0
pittieri	2	1	2	1	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0
cylindrica	1	1	3	1	0	0	1	1	1	0	0	1	1	0	0	1	0	1	0	0
hickeyi	1	1	1	1	1	0	1	1	1	0	0	1	1	0	0	1	0	0	0	0
puberulenta	2	1	?	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0
alata	3	1	?	1	1	0	0	1	2	0	0	1	0	0	0	0	2	0	0	0
aequatoriana	2	1	3	1	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0
appressa	3	1	?	1	1	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0
altescandens	3	1	3	1	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0
gomezii	3	1	3	1	1	0	0	1	1	0	2	1	1	0	0	3	0	0	0	0
osmundacea	2	1	3	0	1	0	?	1	1	0	1	1	1	0	0	1	0	0	0	0
cyathifolia	2	1	3	0	1	0	0	1	2	0	1	1	1	0	0	1	0	0	0	0
latisquamosa	1	1	?	0	1	0	1	1	1	0	1	1	2	0	0	1	0	0	0	0
sessilisora	2	1	1	0	1	0	0	1	1	0	1	0	1	0	0	2	0	0	0	0
canaliculata	1	1	2	0	1	0	0	1	1	0	2	1	1	0	0	0	0	0	0	0
semipinnata	3	1	3	0	1	0	0	1	1	0	0	1	2	0	0	1	0	0	0	0
speciosa	2	1	3	0	1	0	0	1	0	1	0	1	2	1	0	1	0	0	0	0
pilosa	2	1	3	0	1	0	0	0	0	1	0	1	2	1	0	1	0	0	0	0
ancestor	3	1	1	0	1	0	0	1	1	0	1	1	0	1	0	1	0	0	0	0

TABLE 6. Characters and character states used in the cladistic analysis of 35 species of *Polybotrya*. The numbers given to each character state correspond with those shown on one of the cladograms in Figure 14.

1. Dissection of sterile leaves (Fig. 14a). 0 = 4-pinnate; 1 = 3-pinnate-pinnatifid; 2 = 3-pinnate; 3 = 2-pinnate-pinnatifid; 4 = 2-pinnate; 5 = 1-pinnate.
2. Venation (Fig. 14b). 0 = close and long-parallel; 1 = obliquely ascending; 2 = anastomosing.
3. Type of fertile leaf (Fig. 14c). 1 = botryoid, but with lamina not completely reduced; 2 = fully botryoid; 3 = coenosoric; 4 = caudate.
4. Pinnule arrangement (Fig. 14d). 0 = anadromic; 1 = catadromic.
5. Symmetry of pinnule base (Fig. 14b). 0 = symmetrical and truncate; 1 = prolonged acroscopically and truncate; 2 = symmetrical and cuneate.
6. Submarginal connecting strand (Fig. 14e). 0 = absent; 1 = several connections; 2 = present.
7. Stem scale base (Fig. 14d). 0 = attached by a single point; 1 = attached across the width of the base.
8. Hair type (Fig. 14b). 0 = long, acicular; 1 = small, jointed; 2 = uncinate.
9. Pubescence of laminar surface (Fig. 14b). 0 = both surfaces pubescent; 1 = glabrous; 2 = abaxial surface pubescent.
10. Pubescence of laminar margin (Fig. 14d). 0 = glabrous; 1 = ciliate.
11. Pubescence of costae (Fig. 14b). 0 = uniform and dense pubescence; 1 = moderately pubescent or with scattered hairs; 2 = glabrous.
12. Lamina base (Fig. 14b). 0 = deltate; 1 = reduced; 2 = cuneate.
13. Scale color (Fig. 14f). 0 = golden or yellow; 1 = brown; 2 = reddish or bright castaneous; 3 = cream or whitish.
14. Receptacular hairs (Fig. 14d). 0 = unbranched; 1 = branched.
15. Size of lamina (Fig. 14d). 0 = > 1 meter; 1 = < 1 meter.
16. Costal scale type (Fig. 14f). 0 = flaccid and ovate; 1 = linear to narrowly lanceolate; 2 = linear and tortuous; 3 = caducous.
17. Apex of sterile leaf (Fig. 14d). 0 = pinnatifid; 1 = subconform.
18. Stem habit (Fig. 14d). 0 = hemiepiphytic; 1 = terrestrial.
19. Shape of the tertiary pinnules (Fig. 14b). 0 = ligulate; 1 = oblong or ovate; 2 = obovate.
20. Spore size (Fig. 14d). 0 = 40–50 microns long; 1 = 52–56 microns long.

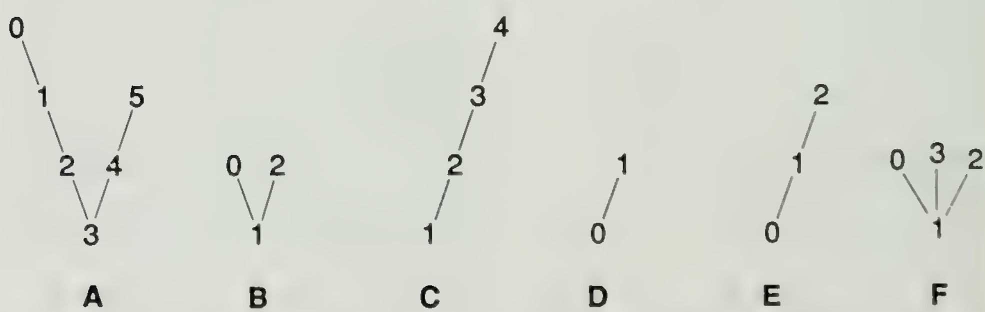

FIGURE 14. Character state trees used in the cladistic analysis of 35 species of *Polybotrya*. Table 6 lists characters and character states. For example, tree B represents the hypothesized evolutionary pathway for character states 2, 11, 12, and 19.

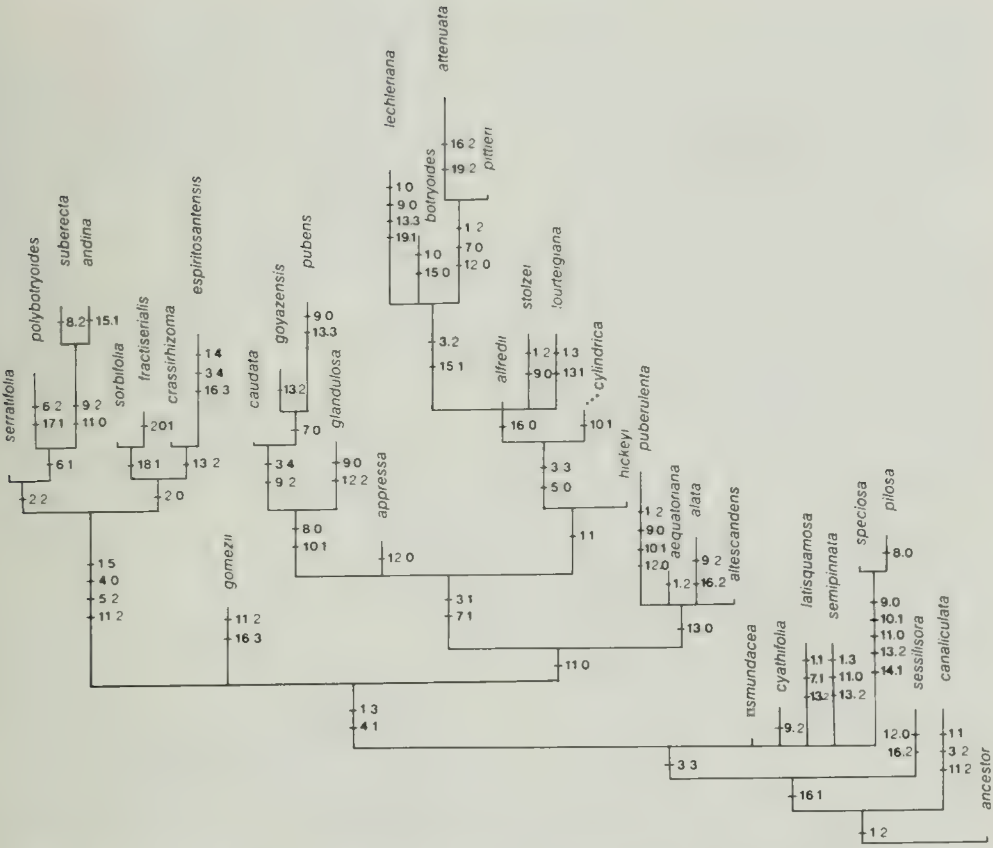

FIGURE 15. Consensus tree for 50 equally parsimonious cladograms of species relationships in *Polybotrya*. The number before the decimal refers to the character; the number after the decimal refers to the character state (Table 6).

Subdivision of the Genus

I subdivide *Polybotrya* into three easily recognized subgenera: 1) *Soromanes*, sterile leaves 1-pinnate, veins anastomosing; 2) *Sorbifolia*, sterile leaves 1-2-pinnate, veins free, close, and parallel; 3) *Polybotrya*, sterile leaves decompound, veins free.

Subgenus *Soromanes* ranges throughout Central America and the Andes, primarily in mountainous areas, but it is conspicuously absent from the Amazon basin and from southeastern Brazil (Maps 1 & 2). This subgenus consists of four well-defined species (species nos. 1–4) that occur in montane forests, primarily from 500–2000 m (Fig. 4).

The only contemporary pteridologist who has maintained *Soromanes* at the generic level is Pichi-Sermolli (1977), who also placed *Soromanes* and *Polybotrya* on separate branches of his phylogenetic diagram, associated with different generic groups. Other pteridologists, such as Christensen (1905), Copeland (1947), and Tryon and Tryon (1982) have subsumed *Soromanes* in *Polybotrya*. My research on both genera has shown that *Soromanes* is the closest genus to *Polybotrya*. Both genera share a unique stem anatomy: a circular grouping of meristeles with each meristele surrounded by a dark, sclerenchymatous sheath (Figs. 6 & 16g). No other fern genus has this unmistak-

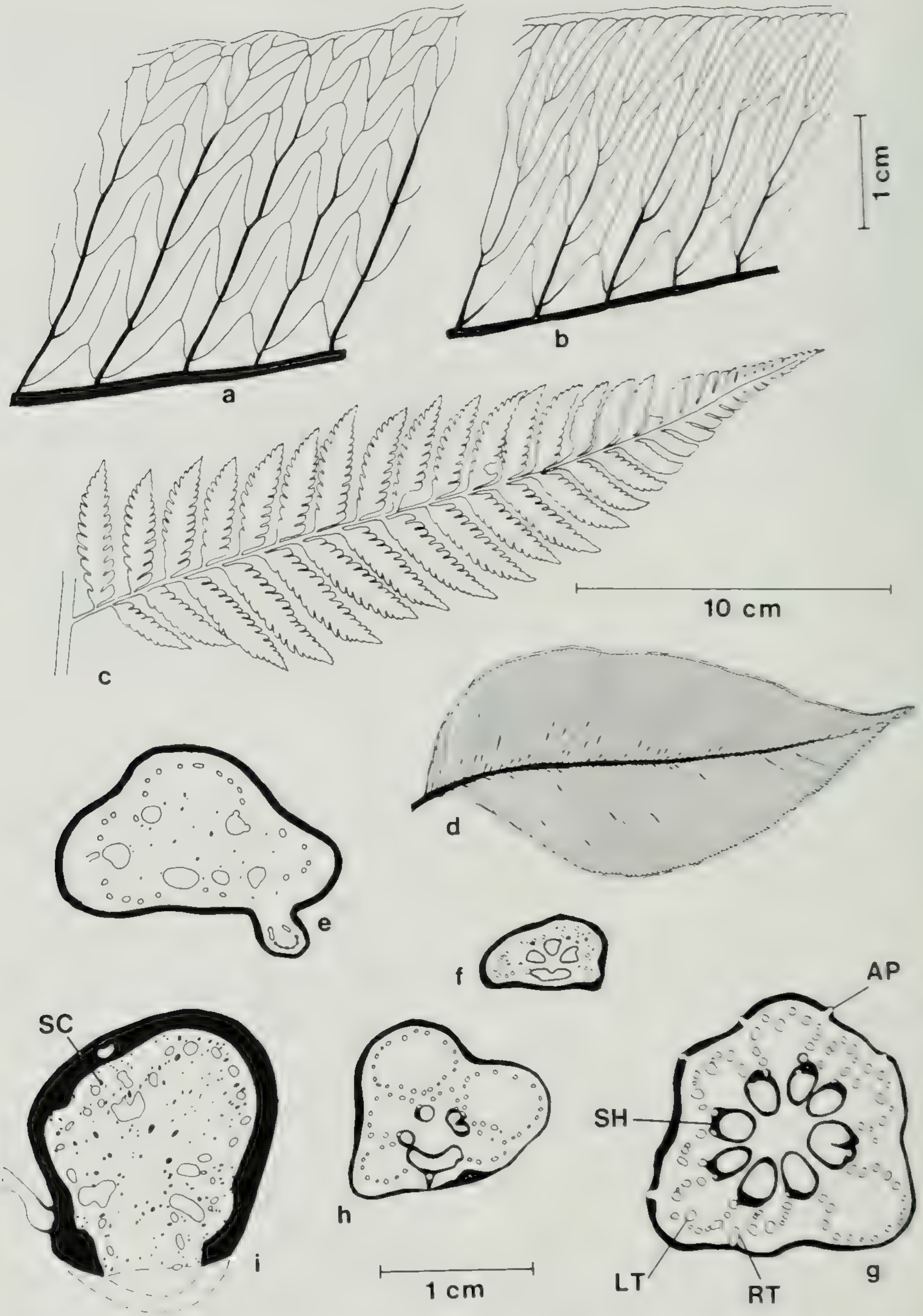

FIGURE 16. *Polybotrya* and closely related genera. a. venation of sterile pinna, *Cyclodium meniscioides*; b. venation of sterile pinna, *Polybotrya polybotryoides*; c. pinna of *Cyclodium trianae* var. *trianae* (compare to *P. sessilisora* and *P. osmundacea*); d. sterile pinna of *Olfersia cervina*, showing venation entirely unlike any *Polybotrya*; e–i. stem cross sections (dorsal surface is up) of e. *Maxonia apiifolia*, f. *Lomariopsis fendleri*, g. *Polybotrya caudata*, h. *Bolbitis lindigii*, i. *Olfersia cervina*. AP aerophore; LT leaf trace; RT root trace; SH sclerenchyma sheath; SC sclereid or stone cell.

able stem anatomy, one of the hallmarks of *Polybotrya*. Other compelling similarities, such as holodimorphic leaves, long-creeping and densely scaly stems, petiole anatomy, and spore morphology, further demonstrate that *Soromanes* and *Polybotrya* are closer genealogically to each other than to any other genus; that is, they are sister groups. In my opinion, these similarities justify including *Soromanes* in *Polybotrya*.

Subgenus *Sorbifolia* is primarily South American (Maps 3 & 4) and consists of four species (species nos. 5–8) that occur in low-elevation forests primarily from 0–1200 (1500) m (Fig. 4). Two species, *P. sorbifolia* and *P. fractiserialis*, are very closely related and contrast sharply with the rest of the genus because of their terrestrial stems. These two species also have distinctive venation: the veins are long, parallel, and sharply ascending (Figs. 24 & 25). The third species, *P. crassirhizoma*, is dissimilar from the others and has dull orange stem scales and slightly more spreading veins (Fig. 26). It is an abundant fern in the western Amazon basin, from Colombia south to Bolivia. *Polybotrya espiritosantensis* is included in this subgenus, even though its leaves are 2-pinnate because its venation (Fig. 27b) is exactly like that of *P. fractiserialis* (Fig. 25e); this similarity suggests a close relationship.

The species having decompound leaves, all free veined (species nos. 9–35), make up the subgenus *Polybotrya*, which is further subdivided into four species groups. Since I see no purpose in giving these groups formal taxonomic names, I informally refer to them with the name of a typical, widespread species for each group, e.g., the "*P. caudata* group." The first three groups described below have catadromic pinnules; the fourth has anadromic pinnules. Pinnule arrangement, however, cannot be used to classify the species groups at a higher level because no other characters correlate with it.

The *P. caudata* group (species nos. 9–12) is the most distinctive because it has peculiar, caudate fertile pinnules that are soriferous on both surfaces, that is, amphiacrostichoid. Actually, what looks like the adaxial soriferous surface is the expanded, thickened margin of the receptacle; the true, phylogenetic, adaxial surface is reduced to a thin green line (see Morphology and Anatomy section). In addition to this diagnostic sorus, the group is further united by the presence of whitish, septate, acicular hairs (Fig. 10a,f,i). *Polybotrya glandulosa* is tentatively assigned to this group because of similarities in leaf cutting and pubescence; however, it has botryoid fertile leaves. This character is constant in *P. pubens*, but both *P. caudata* and *P. goyazensis* can be glabrous. The *P. caudata* group is most frequent and abundant at low elevations from 0–1000 m, although *P. caudata* itself occasionally occurs up to 1900 m (Fig. 4).

The second species assemblage, the *P. alfredii* group, consists of eight primarily Andean species (species nos. 13–20). This group has a characteristic appearance, although it is difficult to describe because few features are constant. In general, the pinnae are short-stalked and crowded near the costa and rhachis. The pinnae bases are more or less equilateral and not acroscopically prolonged as in the rest of the genus. The tertiary segments are often oval or rounded, never narrow or strap-shaped. The grooves of the costules are either truncated by the ridges of the costa or very weakly admitted to the groove of the costa (see Morphology and Anatomy section). Most species in the *P. alfredii* group have botryoid fertile leaves.

The third species group, the *P. altescandens* group, consists of seven species (species nos. 21–27). These species, with the exception of one endemic to the mountains of Costa Rica, grow in the Andes at slightly higher altitudes than the rest of the genus (Fig. 4). This group has pinnule bases slightly to strongly asymmetric, a characteristic that helps to distinguish it from the *P. alfredii* group.

The fourth species group centers on the type of the genus, *P. osmundacea*, and differs from the rest of the genus by having anadromically arranged pinnules. As shown in the illustrations, the species (species nos. 28–35) are very similar in dissection of the leaf. The

pinnule base ascends obliquely on the basiscopic side and prolongates conspicuously on the acroscopic side. This asymmetry imparts a distinctive appearance to the pinnule base (Fig. 48).

Relationships with Other Groups

Pteridologists have always classified *Polybotrya* with *Dryopteris* and such closely related genera as *Arachniodes*, *Cyclodium*, *Cyrtomium*, *Maxonia*, *Olfersia*, *Polystichopsis*, *Polystichum*, and *Stigmatopteris*. These genera share the following features with *Polybotrya*: base chromosome number $x = 41$, dryopteroid costa-costule architecture, spores monolete with prominently inflated perisporial folds, more than three vascular bundles in the petiole, and petioles and petiolules not articulate at their bases.

Familial Relationships

The dryopteroid genera are most closely related to the tectarioid ferns, such as *Ctenitis*, *Lastreopsis*, and *Tectaria*. These genera constitute a natural group on the basis of their costa-costule architecture and special "*Ctenitis*-hairs." As noted in the Morphology and Anatomy section of this monograph, *Polybotrya* lacks *Ctenitis*-hairs, and their absence argues strongly against a close relationship with the tectarioid genera. Furthermore, *Polybotrya* has costa-costule architecture of the dryopterioid type rather than the tectarioid type.

Polybotrya might possibly be construed as a member of the Lomariopsidaceae. Three genera of Lomariopsidaceae—*Lomagramma*, *Lomariopsis*, and *Teratophyllum*—closely resemble *Polybotrya* in overall habit because they have densely scaly, high-climbing stems, strongly differentiated sterile and fertile leaves, and nonindusiate, acrostichoid sori. Furthermore, at the anatomical level, the three genera have diplodesmic venation and dark, sclerenchymatous sheaths surrounding each meristele in the stem. Although no pteridologist has ever classified *Polybotrya* with the Lomariopsidaceae, these similarities prompt me to consider the possibility.

Stem anatomy is tremendously important in the taxonomy of *Polybotrya* and the Lomariopsidaceae. The stem anatomy of *Polybotrya* is unique and has been thoroughly described in the Morphology and Anatomy section. The stem anatomy of the Lomariopsidaceae is also unique among ferns because it has a broad, strap-shaped, ventral meristele that differs from the remaining circular or oblong meristeles (Fig. 16f,h). Like *Polybotrya*, each meristele is surrounded by a dark, sclerenchymatous sheath. This elongated ventral meristele creates a dorsiventral dictyostele. Presumably, this ventral meristele was formed during phylogeny by the fusion of two, once-distinct meristeles like the upper ones (Holttum 1978). In fact, the two ventral meristeles have not completely fused in *Lomariopsis*, as evidenced by the shallow indentation in the ventral band (Fig. 16f). The ancestor of the Lomariopsidaceae, therefore, had a radially symmetrical dictyostele of several to many, circularly arranged meristeles with each meristele surrounded by a dark, sclerenchymatous sheath. In other words, the ancestral stem anatomy was like that of *Polybotrya*. If one looks at Figure 16g, a cross section of a *Polybotrya* stem, and imagines what it would look like if the two or three ventral meristeles were fused into a single meristele, the result would be a replica of the stem anatomy of the Lomariopsidaceae. This compelling similarity in stem anatomy suggests that *Polybotrya* and the Lomariopsidaceae arose from a similar ancestral stock among the dryopteroid ferns. The possibility also exists, however, that parallel evolution accounts for these similarities in stems adapted for climbing.

The leaf architecture of the two differs, however, and most species of Lomariopsidaceae have simply pinnate leaves. The leaves of *Polybotrya*, like those of most dryopteroid ferns, are primitively decompound. All Lomariopsidaceae, except *Bolbitis*, have articulate leaves and/or pinnae. In

contrast, *Polybotrya* and other dryopteroid genera have nonarticulate leaves and/or pinnae. In the climbing genera *Lomariopsis* and *Teratophyllum*, leaves on the terrestrial portion of the stem (bathyphylls) differ greatly from those on the scandent portion (acrophylls). In *Lomariopsis*, the bathyphylls are less divided (usually simple and entire) than the acrophylls, and in *Teratophyllum* they are more dissected than the acrophylls. In *Polybotrya*, however, the bathyphylls and acrophylls are about the same size and shape.

Venation is yet another difference. Several kinds of venation occur in the three genera of Lomariopsidaceae most similar to *Polybotrya*. *Teratophyllum* has simple or forked veins, as does *Lomariopsis*, except that the veins of the former unite with the cartilaginous margin (Holttum 1978). *Polybotrya* also has free veins, but the pattern is entirely different from that of these two genera, as can be seen by comparing the illustrations in this monograph with those shown by Holttum (1978, Figs. 1–8). The veins of *Lomagramma* differ completely from those of these three genera; its veins form a network of three or more rows of oblique areoles without main veins. Venation, therefore, does not support a relationship between *Polybotrya* and the Lomariopsidaceae.

In summary, *Polybotrya* and some genera of Lomariopsidaceae share the following characteristics: climbing stems, dimorphic sterile and fertile leaves, diplodesmic veins, and dark sclerenchymatous sheaths surrounding each meristele. The two groups, however, contrast sharply in such features of leaf architecture as the amount of dissection, pinnae articulation, acrophylls versus bathyphyll differences, venation patterns, and stem anatomy. This conflicting evidence is difficult to assess. Certainly, the climbing habit, sterile-fertile leaf dimorphy, and diplodesmic veins have arisen many times in ferns, but the similarity in stem anatomy is less easily explained. I suspect, however, that the Lomariopsidaceae may have had a separate origin among the dryopteroid ferns, apart from *Polybotrya*. Strong evidence exists that *Polybotrya* was derived from a *Cyclodium*-like ancestor (see below).

Relation to Similar Dryopteroid Genera

Maxonia. This monotypic genus was first described by Christensen (1916), who observed that his new genus "must stand between *Polybotrya* and certain species of *Dryopteris* grouped with *D. amplissima* [*Arachniodes*]." Copeland (1947) also held that *Maxonia apiifolia* (Swartz) C. Chr. represented a phylogenetic intermediate between *Arachniodes* and *Polybotrya* (Fig. 17), and most later pteridologists have agreed that *Maxonia* is intimately related to *Polybotrya*.

Maxonia and *Polybotrya* appear very similar because both have highly differentiated sterile and fertile leaves and densely scaly, climbing stems. Nevertheless, a comparison of stem anatomy shows some important differences (Fig. 16e,g). The most evident dissimilarity is that each meristele of *Maxonia* is not surrounded by a dark sclerenchymatous sheath as in *Polybotrya*. Also, the dictyostele of *Maxonia* is dorsiventral (Chandra 1975; Walker 1972), unlike that of *Polybotrya*, which is radially symmetrical. Clearly, *Maxonia* lacks the stem anatomy that characterizes *Polybotrya*, thus weakening the hypothesis that these genera are closely related.

Strong evidence exists that *Maxonia* is most closely related to the American species of *Arachniodes*, in particular *A. macrostegia* (Hooker) Tryon and Conant. Indeed, if *Maxonia apiifolia* had monomorphic leaves it would without doubt be placed in *Arachniodes*. The similarities between the two genera are striking and are best seen in the sterile leaves. Both genera have pinnules arranged anadromically, basal pinnae elongated basiscopically, and laminae broadened notably at the base and of similar thickish texture. In addition, the pinnules and smaller segments have cuneate bases and acute apices, thereby imparting a characteristic "streamlined" appearance to the lamina that

contrasts sharply with the truncate or acroscopically prolonged bases and rounded apices in *Polybotrya*. Both *Maxonia* and *Arachniodes* have costa-costule architecture of the dryopteroid type (grooves decurrent into each other; Holttum 1984). Finally, both genera have remarkably similar brown, thickish, round-reniform indusia.

The evolution of the climbing stem of *Maxonia* poses no problem if *Arachniodes* is accepted as the ancestor. Since the American species of *Arachniodes* have creeping stems, the potential to evolve a fully hemiepiphytic stem, as in *Maxonia*, was initially present and easily achieved.

In short, *Maxonia* is similar to *Polybotrya* because it arrived at a comparable evolutionary grade or level, but it came from a different source (Fig. 17). *Polybotrya* was probably derived from *Cyclodium* (see below), and *Maxonia* from *Arachniodes*, probably from an ancestor close to *A. macrostegia*. *Maxonia* should not, however, be subsumed with *Arachniodes* because it is derived from it. It is convenient, and certainly in harmony with past taxonomic practice, to distinguish *Maxonia* generically on the basis of its leaf dimorphism and climbing stem.

Olfersia. This genus consists of a single species, *O. cervina* (L.) Kunze, the placement of which has been controversial. Most recently, pteridologists have placed *Olfersia* in *Polybotrya* because both have strongly dimorphic sterile and fertile leaves, nonindusiate sori, similar perispore morphology, and densely scaly, creeping stems. Yet *Olfersia* differs from *Polybotrya* by its venation, conform apical pinna, and stem anatomy. Moran (1986) studied *Olfersia* and concluded that it and *Polybotrya* are sister taxa best maintained in separate genera.

Cyclodium (*sensu* Smith 1986). *Polybotrya* was probably derived from an ancestor which, if it were alive today, would be placed in *Cyclodium*. This genus has two important prerequisites for the evolution of *Polybotrya*. First, the fertile leaves of *Cyclodium* are slightly to strongly dimorphic. Second, the stem is creeping in all species of *Cyclodium*, and in several species it becomes fully hemiepiphytic. *Cyclodium*, therefore, has the genetic capacity to evolve two cardinal features of *Polybotrya*: holodimorphic sterile and fertile leaves and a climbing stem.

Moreover, *Cyclodium* contains species that look remarkably like certain species of *Polybotrya*. The 2-pinnate-pinnatifid leaf of *C. trianae* (Mett.) A.R. Smith var. *trianae* is strikingly like some species of *Polybotrya* with respect to cutting and venation (cf. Fig. 16c to *P. caudata*, *P. osmundacea*, and *P. sessilisora*, Figs. 28, 47, & 51, respectively). In fact, several times during fieldwork in Ecuador, I mistook sterile leaves of *C. trianae* for terrestrial leaves of *P. caudata*. Similarity is also seen in the simply pinnate lamina of *C. meniscioides* (Willd.) Presl, which has anastomosing venation notably like that found in *Polybotrya* subgenus *Soromanes* and is also simply pinnate (Fig. 16a,b). This similarity of venation was noted long ago by Hooker and Baker (1874). I am not suggesting that these two species of *Cyclodium* gave rise to *Polybotrya*, but within both genera, species have evolved with similar characteristics, and this homologous vari-

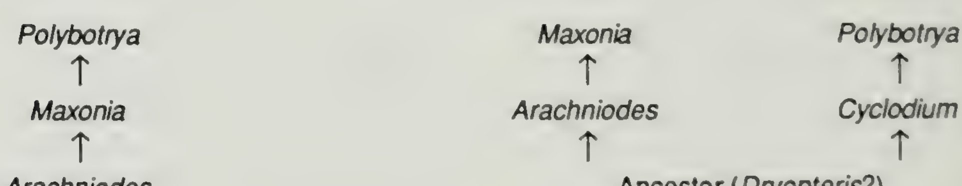

FIGURE 17. Two phylogenetic hypotheses concerning the relationships of *Maxonia* and *Polybotrya*: left, the hypothesis proposed by Christensen (1916); right, the hypothesis proposed here. See text for explanation of characters involved.

ation implies a close genetic relationship. In conclusion, the close relationship between *Cyclodium* and *Polybotrya* is evidenced by their mutual possession of dimorphic leaves, creeping stems, similar evolutionary tendencies, and, at least in some species, remarkably similar leaf dissection and venation.

Part Two: Taxonomic Treatment

In evolutionary biology almost all phenomena and processes are explained through inferences based on comparative studies. These, in turn, are made possible by very careful and detailed descriptive studies. It is sometimes overlooked how essential a component in the methodology of evolutionary biology the underlying descriptive work is.

Ernst Mayr (1982)

Notes on the Presentation of Data

In most cases, the key can be used with specimens lacking fertile leaves. Fertile leaves, however, are often helpful in identification and are given as additional characters in many couplets. The key will generally not work when leaves are less than 45 cm long. To facilitate the comparison of similar species, I have arranged the species phylogenetically rather than alphabetically. The synonymy given for each species is complete. I have kept the descriptions short by not repeating characteristics that are constant for the genus. For example, all species of *Polybotrya* have a pinnatifid leaf apex; this characteristic is mentioned only in the generic description and is not repeated in each species description. The distribution maps (see appendix) were compiled from the specimens listed in the Specimens Examined section in each species treatment. In some cases, I could not find localities despite searching various atlases, indices, and gazetteers.

The terms *basiscopic* and *acroscopic* are used frequently in the key and in descriptions to refer to the sides of pinnules (Fig. 18). The acroscopic side of a pinnule is the side directed toward the apex of the pinna bearing the pinnule. Conversely, the basiscopic side of a pinnule is that side directed toward the pinna base and rhachis. Two other frequently used terms, *catadromic* and *anadromic*, refer to pinnule arrangement. The pinnule arrangement is catadromic when the pinnule closest to the rhachis is basiscopic; when the pinnule closest to the rhachis is acroscopic, the arrangement is anadromic (Fig. 18). I have de-

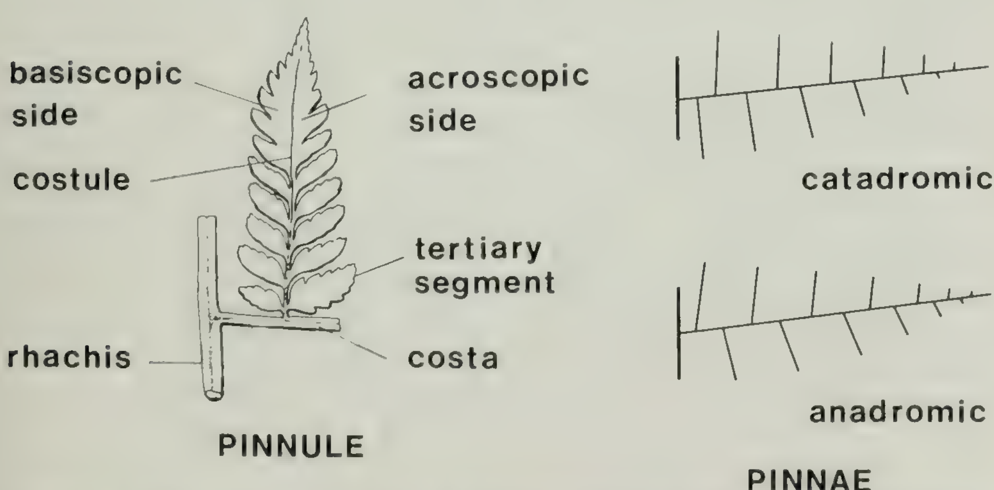

FIGURE 18. Terms frequently used to describe the leaves of *Polybotrya*. See text for further explantions.

fined the specialized terms that refer to the fertile leaves, such terms as *botryoid*, *coenosoric*, and *amphiacrostichoid*, in the Morphology and Anatomy section and in the Description of the Genus section.

Description of the Genus

POLYBOTRYA WILLD.

Polybotrya Willd., Species Plantarum, ed. 4. 5:99. 1810. Type species: *Polybotrya osmundacea* Willd.

Soromanes Fée, Mém. Fam. Foug. 2 (Hist. Acrost.) 16. 1845.Type species: *Soromanes serratifolium* Fée = *Polybotrya serratifolia* (Fée) Klotzsch.

Botryothallus Klotzsch, Bot. Zeit. 4:104. 1846. *nom. nudum*. Type species: *Botryothallus kunzei* Klotzsch *nom. nudum* = *Polybotrya serratifolia* (Fée) Klotzsch.

Stem hemiepiphytic, long-creeping, or (two species) terrestrial and short-creeping, 1.0–3.5 cm wide (excluding scales), the scandent portions unbranched, the terrestrial portions occasionally branched; dictyostelic, in cross section with a characteristic pattern of 4–10 circularly arranged meristeles, each meristele surrounded by a dark sclerenchyma sheath; *aerophores* present in most (all?) species, continuous and decurrent from the lateral aerophores of the petiole, darkening upon drying and not visible in herbarium specimens, in fresh material appearing yellowish, linear, 1–3 mm wide, slightly raised and bearing stomata; *rootlets* produced only on the ventral surface; *scales* numerous, densely covering the stem, spreading or appressed, primarily of two general types: 1) thick, dark brown, opaque, margins entire, attached across the length of the curved, thickened base, and 2) thin, variously colored (ranging from yellow, orange, red to brown), translucent, margins denticulate or highly erose, attached at a central, basal point. **Sterile leaves** up to 2.0 m long, reclining when mature, internodes generally 10–15 cm apart, bulbils lacking; *petiole* with 8–16 vascular bundles arranged in a mushroomlike outline, the base decurrent for a short distance on the stem, scaly, with scales shorter and wider than those on the stem, the aerophores present laterally as thin yellowish green lines, the adaxial surface slightly flattened, trisulcate in dried material; color stramineous, light green or darkened abaxially; *rhachis* trisulcate below becoming unisulcate above, the groove pubescent within; *lamina* papyraceous to subcoriaceous, 1-pinnate (subgenera *Soromanes* and *Sorbifolia*) or 1-pinnate-pinnatifid to 4-pinnate (subgenus *Polybotrya*), usually lanceolate, the base rarely deltate or cuneate, the apex pinnatifid; *pinnae* not articulate to the rhachis, linear, lanceolate or deltate, symmetrical or slightly prolonged acroscopically, a few species having the basal pair slightly prolonged basiscopically; *pinnules* arranged catadromically or anadromically, symmetrical or asymmetrical at the base, if asymmetrical then with the basiscopic side reduced and oblique and the acroscopic side prolonged; *grooves of costules* decurrent into the the grooves of the costa or truncated by the ridges of the costa and therefore not decurrent (intermediates exist); *veins* free or (in subgenus *Soromanes*) anastomosing, ending close to the margin, hydathodes absent; *hairs* of two types: 1) all species have tiny, reddish, appressed, jointed, flattened hairs on the lamina that grade into the scales (these actually represent reduced scales), and 2) most species have hairs that do not intergrade with the scales, these are whitish and cylindrical, ranging from unicellular and less than 0.1 mm long to 15 cells and 2.0 mm long, or uncinate. **Fertile leaves** appearing as a skeletonized version of the sterile, more ephemeral than the sterile, produced only on the scandent portion of the stem in hemiepiphytic species; *sori* nonindusiate and of three types: 1) round, discrete, usually at the tips of pinnately arranged stalks (botryoid type), 2) oblong or linear formed by the fusion of several different sori (coenosoric type), and 3) sori apparently occupying both surfaces of a caudate pinnule (amphiacrostichoid type); *diplodesmic veins* present except in botryoid sori; *sporangia* with 64 spores per capsule, the capsule glabrous except in *P. pubens* which has setose hairs at the apex near the annulus; sporangial stalks with three rows of cells at the apex, two-rowed below, paraphysate in most species by lateral hairs, these multicellular and unbranched (branched only in *P. speciosa*); annulus of 15–22 indurated cells; *spores* (32)45–65(80) microns long, dark brown when viewed with transmitted light under a compound microscope, deep orange when viewed with reflected light under a dissecting microscope, monolete, aperature linear and ⅓–¾ the length of the long axis, exospore smooth, perispore bilayered with inflated folds and echinate to various degrees. $x = 41$.

Key to the Species of Polybotrya

1. Sterile leaf 1-pinnate.
   2. Veins of sterile leaf anastomosing (subgenus *Soromanes*).
      3. Plants of Mesoamerica; vein tips joined into a faint, continuous, submarginal connecting strand. .... 2. *P. polybotryoides*, p. 80.
      3. Plants of South America and Trinidad; vein tips usually, but not always, free.
         4. Lamina pubescent abaxially with uncinate hairs. Western cordillera of Ecuador.
            5. Hairs on abaxial surface 0.1–0.3 mm long, colorless, erect, 1–3 celled; free pinnae pairs 6–13 below the pinnatifid apex, mostly 15–21 × 4–5 cm. .... 3. *P. suberecta*, p. 50.
            5. Hairs on abaxial surface 0.5–1.2 mm long, tawny, spreading, 5–12 celled; free pinnae pairs 4–7 below the pinnatifid apex, mostly 17–33 × 5.7–10 cm. .... 4. *P. andina*, p. 50.
         4. Lamina glabrous abaxially.
            6. Apex evenly pinnatifid, not similar to the lateral pinnae (Fig. 20a); vein tips free or incompletely anastomosing.
               7. Stem scales linear, stiffish, mostly 0.3–1.0 mm wide, usually opaque and concolorous; fertile pinnules more than 2.0 cm long. Colombia, Ecuador, and Peru. .... 3. *P. suberecta*, p. 50.
               7. Stem scales lanceolate, flaccid, mostly 1–2 mm wide, often with a dark central stripe and lighter borders; fertile pinnules generally less than 2.0 cm long. Andes of Venezuela; Trinidad. .... 1. *P. serratifolia*, p. 43.
            6. Apex subconform, similar to lateral pinnae, or with one or a few small basal lobes (Fig. 20b,c); vein tips joined into a faint continuous submarginal connecting vein (see text for observation of this character). Southern Mexico to Peru. .... 2. *P. polybotryoides*, p. 80.
   2. Veins of sterile leaf free (subgenus *Sorbifolia*).
      8. Stem terrestrial and short-creeping; scales brown, essentially concolorous; fertile pinnules commonly round or oblong, usually less than 1 cm long.
         9. Largest pinnae 7–10 times longer than broad, abaxial surface often with white or light brown, sessile, globose glands; apex of 3–7 pinnalike lobes (Fig. 24a), these with long decurrent bases; stem scales shiny brown, mostly transparent and denticulate; spores 40–47 microns long. .... 5. *P. sorbifolia*, p. 53.
         9. Largest pinnae 5–7 times longer than broad, abaxial surface without glands; apex of 2 or 3 lobes, their bases not long decurrent (Fig. 25b,c); stem scales dull brown, mostly opaque with entire or subentire margins; spores mostly 52–56 microns long. .... 6. *P. fractiserialis*, p. 54.
      8. Stem hemiepiphytic and long-creeping; scales reddish brown or orange, with a prominent central stripe and lighter borders; fertile pinnules linear and usually more than 1 cm long. .... 7. *P. crassirhizoma*, p. 58.
1. Sterile leaves 1-pinnate-pinnatifid to 4-pinnate (subgenus *Polybotrya*).
   10. Pinnules of medial pinnae catadromic (Fig. 18).
      11. Rhachis and costae pubescent, hairs 1.0–2.5 mm long. Amazonian lowland forests.
         12. Lamina more than 15 cm wide at the base; petiole more than 15 cm long; largest pinna lobes with entire margins; stem scales usually denticulate, translucent, cream to castaneous; fertile pinnules caudate, 3–15 mm wide, sori acrostichoid, apparently covering both surfaces; sporangial capsules setose (Fig. 30e,f). .... 11. *P. pubens*, p. 68.
         12. Lamina up to 10 cm wide at the base; petiole up to 4 cm long; largest pinna lobes with serrate margins; stem scales entire, dark, and opaque; fertile pinnules botryoid, sori round, discrete, 1–3 mm wide; sporangial capsules glabrous. .... 12. *P. glandulosa*, p. 71.
      11. Rhachis and costae glabrous, or if pubescent, hairs shorter than 1 mm long. Amazonia and elsewhere.

13. Ultimate segments or lobes of sterile leaf 0.5–1.5 mm wide *and* only one-nerved; lamina often pubescent on both surfaces. Andes of Colombia to Bolivia, Guyana. .... 13. *P. lechleriana*, p. 71.
13. Ultimate segments or lobes of sterile leaf more than 1 mm wide and with several nerves; lamina rarely pubescent on both surfaces.
    14. Stem scales bright golden or yellowish *and* the pinnatifid portions of the pinnae or pinnules with a single veinlet running towards the sinus arising directly from the costa or costule between the main lobes or vein groups (Fig. 45d). Andes of Colombia to Peru. .... 26. *P. altescandens*, p. 97.
    14. Plants without the above combination of characters.
        15. Laminar margins sparsely ciliate, hairs minute, less than 0.1 mm long (Fig. 28a) *and* fertile pinnules caudate, sori amphiacrostichoid, covering both surfaces of the leaf.
            16. Stem scales dull brown, opaque, appressed-ascending, margins subentire, base curved and thickened (Fig. 28h). Widespread. .... 9. *P. caudata*, p. 60.
            16. Stem scales shiny reddish to castaneous, membranous, spreading, margins denticulate, base usually cordate at point of attachment (Fig. 29f). Paraguay and Brazil. .... 10. *P. goyazensis*, p. 66.
        15. Laminar margins glabrous, or if sparsely ciliate, fertile pinnules not caudate and sori not amphiacrostichoid.
            17. Abaxial surface of sterile leaf pubescent, hairs fine, erect, whitish, less than 0.1 mm long *and* costae scaly with numerous, golden brown, tortuous scales. Panama. .... 23. *P. alata*, p. 92.
            17. Plants without the above combination of characters. Panama and elsewhere.
                18. Plants nearly glabrous throughout, even within the grooves *and* pinnule margins cut less than ⅔ of the way to the costule. Costa Rica. .... 27. *P. gomezii*, p. 99.
                18. Plants usually pubescent on the major axes and within the grooves; pinnules cut more than ⅔ of the way to the costule.
                    19. Lamina margins sparsely ciliate, hairs 0.1 mm long *and* stem scales opaque, appressed, the base curved and thickened. Southeastern Brazil. .... 20. *P. cylindrica*, p. 86.
                    19. Lamina margins glabrous; stem scales as above or thin, spreading, and translucent. Plants not from southeastern Brazil.
                        20. Pinnule bases more or less symmetrical (Fig. 35); tertiary segments often inserted at about right angles to the costule, ovate to oblong, usually less than 2.5 (3.0) times longer than broad.
                            21. Pinnules up to 2.5 × 1.2 cm, with only 5–7 segments and/or lobes; lamina up to 55 × 26 cm, apex long-attenuate; major axes with narrow, dark, tortuous scales. Colombia. .... 14. *P. attenuata*, p. 74.
                            21. Pinnules larger than 2.5 × 1.2 cm, with more than 5 segments and/or lobes; lamina often larger than 55 × 26 cm, apex rarely long-attenuate; major axes rarely with narrow, dark, tortuous scales.
                                22. Sterile lamina slightly reduced at the base; basal pinnae less than 3.5 times longer than broad, usually elongated basiscopically; fertile leaves coenosoric; sori not stipitate but placed close to the midrib.
                                    23. Sterile lamina pubescent adaxially. Colombia. .... 15. *P. stolzei*, p. 76.
                                    23. Sterile lamina glabrous adaxially.
                                        24. Margins of tertiary segments entire to crenate, serrate or lobed; pinnules of medial pinnae cut more than half way to the costule for most of their length in pinnae 25 cm or longer. Mesoamerica, Ecuador, and Bolivia. .... 16. *P. alfredii*, p. 78.

24. Margins of tertiary segments entire, never crenate, serrate, or lobed; pinnules of medial pinnae cut less than half way to the costule for most of their length. Colombia. ... . 18. *P. lourteigiana*, p. 82.

22. Sterile lamina broadest at the base; basal pinnae 3.5–4.0 times longer than broad, not strongly elongated basiscopically; fertile leaves botryoid; sori stipitate, stalks 1–4 mm long. Colombia. .... 19. *P. pittieri*, p. 84.

20. Pinnule bases acroscopically prolonged (Fig. 44); tertiary segments and lobes usually inserted obliquely to the costule, somewhat elongate and falcate, more than 2.5 times longer than broad.

25. Costal scales scattered, dark, ovate to lanceolate, flaccid (Fig. 52b); fertile leaves botryoid (Fig. 52c). Cloud forests of northern Venezuela. .... 32. *P. canaliculata*, p. 111.

25. Costal scales absent, or if present, then linear, tortuous; fertile leaves rarely botryoid.

26. Sterile lamina 3–4-pinnate-pinnatisect, ultimate segments or lobes 1–2 mm wide; major axes on all sides with numerous, narrow (1–3 cells wide), reddish brown, tortuous, spreading scales; fertile leaves botryoid. Colombia. .... 17. *P. botryoides*, p. 80.

26. Sterile lamina to only 3-pinnate-pinnatifid, ultimate segments or lobes more than 1–2 mm wide; major axes lacking numerous scales, or if scales present, then not as above.

27. Lamina puberulent on both surfaces; veins prominulous. Andes of Ecuador and Bolivia. .... 22. *P. puberulenta*, p. 90.

27. Lamina always glabrous adaxially and usually so abaxially; veins not prominulous.

28. Stem scales dull brown, thick and opaque, attached across the length of the curved and thickened base, margins subentire.

29. Tertiary segments lobed, lamina usually 3-pinnate-pinnatifid.

30. Costae evenly pilosulous, hairs less than 0.1 mm long; costular grooves truncated by the ridges of the costae and therefore not decurrent; grooves glabrous or nearly so within. Andes of Colombia and Bolivia. .... 21. *P. hickeyi*, p. 88.

30. Costae glabrous or with only scattered hairs; costular grooves decurrent into the costal grooves; grooves filled with reddish or brownish hairs. Widespread species. .... 28. *P. osmundacea*, p. 101.

29. Tertiary segments entire or only minutely serrate at the apex; lamina mostly 2-pinnate-pinnatifid. Andes of Ecuador. .... 25. *P. appressa*, p. 94.

28. Stem scales reddish brown or golden, thin and translucent, attached at a central point, base not curved or thickened, margins denticulate to erose.

31. Stem scales reddish brown; lamina with punctate, resinous glands; costal grooves packed with protruding hairs 0.3–0.8 mm long. Guadeloupe and Martinique. .... 29. *P. cyathifolia*, p. 106.

31. Stem scales golden; lamina lacking punctate, resinous glands; costal grooves glabrous. Andes of Ecuador. .... 24. *P. aequatoriana*, p. 94.

10. Pinnules of medial pinnae anadromic (Fig. 18).

32. Stem scales yellowish to golden; lamina usually with a single veinlet springing directly from the costa or costule between the main lobes or vein groups (Fig. 45d). Andes of Colombia, Ecuador, and Peru. .... 26. *P. altescandens*, p. 97.

32. Stem scales brown, castaneous, or reddish; lamina lacking a veinlet as described above.

33. Sterile leaves 2-pinnate; pinnules entire, bases symmetrical and cuneate; fertile pinnules cylindrical and entire. Known only from the state of Espírito Santo, southeastern Brazil. .... 8. *P. espiritosantensis*, p. 60.

33. Sterile leaves 2–4-pinnate; pinnules divided, lobed, or serrate, the bases usually prolonged acroscopically; fertile pinnules lobed and/or divided.

34. Scales of the petiole base 5–6 mm wide, broadly ovate, castaneous. Colombia. ... . 30. *P. latisquamosa*, p. 108.

34. Scales of the petiole base less than 4 mm wide, usually narrowly lanceolate, brown, castaneous, or reddish.
   35. Abaxial surface of lamina evenly pubescent; stem scales reddish. Southeastern Brazil.
      36. Costal hairs less than 1 mm long. .... 34. *P. speciosa*, p. 115.
      36. Costal hairs 1–2(2.5) mm long. .... 35. *P. pilosa*, p. 117.
   35. Abaxial surface of lamina glabrous; stem scales variously colored. Southeastern Brazil and elsewhere.
      37. Fertile leaves botryoid, i.e., all ultimate soriferous segments round and discrete, not fusing to form an oblong or linear sorus (Fig. 52c).
         38. Sterile lamina to 4-pinnate; stem scales dull to unaided eye, dark brown, with entire or subentire margins; costal scales broadly ovate to lanceolate; costae glabrous or more rarely pubescent; hairs short, reddish, less than 0.1 mm long; sori short-stalked (Fig. 52c). Cloud forests, Andes of Venezuela. .... 32. *P. canaliculata*, p. 111.
         38. Sterile lamina to 3-pinnate; stem scales shiny, dark castaneous, with denticulate-erose margins; costal scales narrowly lanceolate to linear; costae often pubescent, hairs 0.5 - 1.0 mm long, whitish; sori sessile (Fig. 51c). Lowland forests, northern Amazon basin and Guiana Highlands. .... 31. *P. sessilisora*, p. 108.
      37. Fertile leaves coenosoric, i.e., some or most of the ultimate soriferous segments, especially those near the apex, fusing to form an oblong to linear sorus (Fig. 47g).
         39. Abaxial surface of costules evenly hirsute, hairs less than 0.1 mm long, or if glabrous, stem scales reddish. Southeastern Brazil.
            40. Stem scales reddish; margins of tertiary segments or lobes crenate to lobed. .. .. 34. *P. speciosa*, p. 115.
            40. Stem scales bright castaneous; margins of tertiary segments or lobes entire. ... . 33. *P. semipinnata*, p. 113.
         39. Abaxial surface of costules glabrous or variously pubescent by soft whitish hairs more than 0.1 mm long; stem scales rarely reddish. Plants not of southeastern Brazil.
            41. Costal grooves glabrous within; sterile lamina mostly 2-pinnate-pinnatifid. Costa Rica. .... 27. *P. gomezii*, p. 99.
            41. Costal grooves pubescent within, hairs reddish to brownish; sterile lamina mostly 3-pinnate-pinnatifid.
               42. Basal acroscopic segment of pinnules usually with a slight basal gibbosity on both margins (Fig. 49c); lamina membranaceous, almost always with reddish punctate glands abaxially. Guadeloupe and Martinique. .... 29. *P. cyathifolia*, p. 106.
               42. Basal acroscopic segment of pinnules lacking basal gibbosity, usually slightly reduced or oblique (Figs. 47 & 48); lamina thicker, papyraceous to chartaceous, rarely with reddish punctate glands abaxially. Widespread. .... 28. *P. osmundacea*, p. 101.

Species Descriptions

POLYBOTRYA subgenus SOROMANES
(Fée) Moran *comb. & stat. nov.*

Soromanes Fée, Mém. Fam. Foug. 2 (Hist. Acrost.) 16. 1845. TYPE SPECIES: *Soromanes serratifolium* Fée = *Polybotrya serratifolia* (Fée) Klotzsch.

Polybotrya section *Soromanes* (Fée) Klotzsch, Linnaea 20:430. 1847.

Polybotrya subgenus *Soromanes* (Fée), attributed incorrectly to Klotzsch by Fée, Genera Filicum 50, invalid.

Acrostichum subgenus *Soromanes* Hooker, Species Filicum 5:256. 1864. TYPE SPECIES: *Acrostichum caenopteris* Hooker = *Polybotrya serratifolia* (Fée) Klotzsch.

Sterile leaves 1-pinnate; *veins* from adjacent costules anastomosing, 4–6 pairs, curved ascending, the basal pair joining ⅓–½ the distance from the margin to the costa, then with an excurrent vein to the base of the above anastomosing pair, the distal veinlets strongly curved towards the apex, vein tips at the margin free or, in *P. polybotryoides*, joined by a submarginal vein. *Fertile pinnae* pectinate.

1. **Polybotrya serratifolia** (Fée) Klotzsch (Fig. 19, Map 1).

Polybotrya serratifolia (Fée) Klotzsch, Linnaea 20:430. 1847.

Soromanes serratifolium Fée, Mém. Fam. Foug. 2 (Hist. Acrost.) 82, tab. 43. 1845. TYPE: P! (3 sheets), in Bory Herbarium, cited by Fée as "*Polybotrya serrata*, Galeotti, in herb. Bory, Habitat in Mexicana republica, Lagunetta (Galeotti). - V.S. in herb. Bory." but probably collected by Linden in Venezuela and later distributed by Galeotti (see text discussion). I have selected as the lectotype that sheet which Fée illustrated for his tab. 43.

Soromanes dentatum Fée, Mém. Fam. Foug. 2 (Hist. Acrost.) tab. 43. 1845. Fée's tab. 43 was erroneously labeled as "*S. dentatum*" instead of *S. serratifolium*. His tab. 43 is a precise illustration of the lectotype of *P. serratifolia*.

Soromanes integrifolium Fée, Mém. Fam. Foug. 2 (Hist. Acrost.) 82, tab. 42. 1845. Fertile leaf only, the sterile one is that of *Cyclodium meniscioides*. TYPE: Alexander Braun Herbarium (B).

Botryothallus kunzei Klotzsch, Bot. Zeit. 104. 1846. *nom. nudum*, cited by Ettingshausen (1864).

Polybotrya kunzei Ettingshausen, Denkschr. Akad. Wien. 22:66, fig. 2. 1864. TYPE: Only "in Colombia" was mentioned.

Acrostichum caenopteris Hooker, Species Filicum. 5:256. 1864. *nom. nov.* for *Soromanes serratifolium* Fée, *non* Kaulf. 1824, with same type.

Polybotrya coenopteris (Hooker) Christ, Farnkr. 44. 1897.

Soromanes coenopteris (Hooker) Christ, Bull. Herb. Boissier, II. 3:613. 1903.

Acrostichum hartii Baker, J. Bot. 371. 1881. TYPE: Trinidad, *Hart 228* (holotype: K, photo at US!; isotype: NY!).

Polybotrya hartii (Baker) C. Chr., Index Filicum. 504. 1906.

Polybotrya crassa Morton, Fieldiana Bot. 28:13. 1951. TYPE: Venezuela. Monagas: south-facing forested slopes above limestone bluffs, northeast of Guacharo, alt. 1300–1400 m, 11 April 1945, *Steyermark 61991* (holotype:US!; isotypes: F!, VEN!).

Stem hemiepiphytic, 1.5–3.0 cm thick; *scales* 0.8–1.5 mm long, 0.5–2 mm wide, narrowly lanceolate, reddish brown to light orange, with or without a prominent dark central stripe, membranous, lustrous, spreading, margins highly erose to merely denticulate at the apex. *Sterile leaves* up to 0.8 m long, dull green adaxially, pale green abaxially, chartaceous to subcoriaceous; *petiole* scaly at base, up to 30 cm long, trisulcate and flattened adaxially; *lamina* up to 50 × 27 cm, 1-pinnate; *pinnae* 6–12 pairs, mostly (7)10–20(23) × (2)3–4.5(5.5) cm wide, lanceolate, base rounded, cuneate to truncate, margins entire to serrate, apex acuminate; *veins* in pinnated groups 3–6 mm apart, the tips arcuate, free; *axes* with a few scattered scales, rarely pubescent, the hairs tiny, less than 0.1 mm long, unicellular, whitish; *grooves* nearly glabrous within. *Fertile leaves* 2-pinnate, often about the same length as the sterile

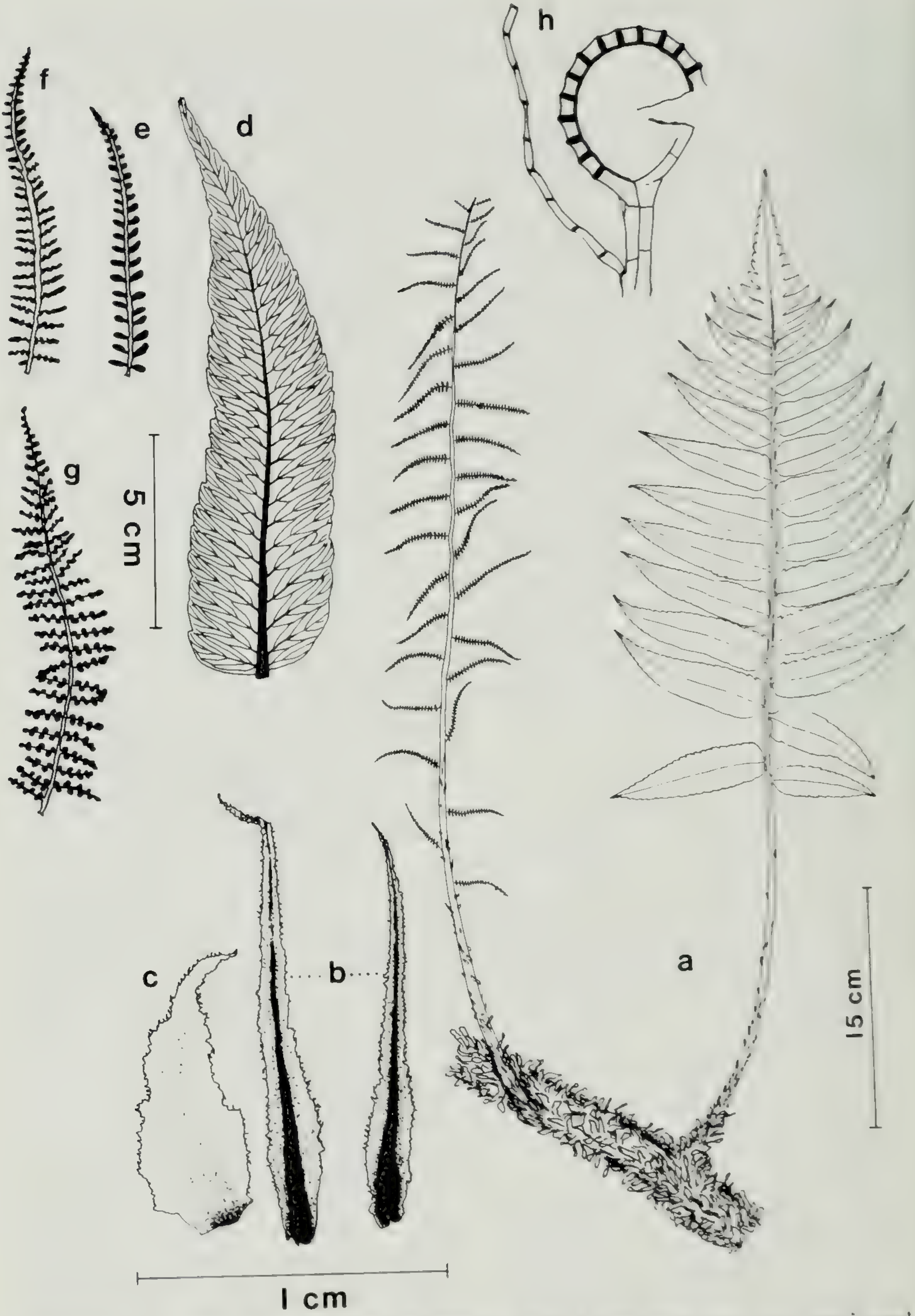

FIGURE 19. *Polybotrya serratifolia* (Fée) Klotzsch. a. habit; b. stem scales (note erose margins and dark central stripes); c. petiole scale; d. sterile pinna; e–g. fertile pinnae showing variation in cutting; h. sporangium with paraphysis. a–c: *van der Werff & Wingfield 3430* (MO). d: *Aristeguieta 3963* (VEN). e: *Fendler 261* (MO). f,h: *Broadway 9947* (GH). g: type, probably *Linden* (P).

leaves; *pinnae* linear to narrowly triangular, evenly long-tapered to apex, up to 14×2.5 cm; *pinnules* entire to occasionally slightly lobate, linear, oblong or sometimes clavate, 4–15(20) mm long, 2–3 mm wide, the adaxial margins folding together at maturity, giving the pinnules a cylindrical appearance; *sori* coenosoric, continuously covering the pinnule, occasionally lobed at the base or botryoid; *sporangial stalks* paraphysate; *spores* (44)50–60(63) microns long. $n = 41$.

Other illustrations: Fée's tab. 43 is an excellent, precise illustration of the lectotype; Vareschi, Fl. Venez., Helechos, vol. 1, tab. 71. 1969 (as *P. crassa*).

Polybotrya serratifolia grows in undisturbed, wet, premontane and cloud forests from 1200–2400 m elevation. It is known only from the mountains of northern Venezeula and Trinidad (Map 1). Van der Werff and Smith (1980) report this species (as *Polybotrya* sp., aff. *crassa*) from the state of Falcón, Venezuela, where it grows in wet premontane forest with another Venezuelan endemic, *P. canaliculata*.

The distinctive, wide, flaccid, erose scales of *P. serratifolia* (Fig. 19b,c) distinguish it from the other species in subgenus *Soromanes*. *Polybotrya serratifolia* differs from the similar *P. polybotryoides* by its submarginal connecting vein. This vein, however, is not easily seen because the connecting vein of *P. polybotryoides* is very faint and the vein tips of *P. serratifolia*, though free, are arcuate and simulate a submarginal connecting vein.

Polybotrya hartii and *P. crassa* are placed in synonymy, although at first sight they look different. Both were originally distinguished from *P. serratifolia* by their more dissected (botryoid) fertile leaves. But these botryoid leaves represent a break-up of the coenosorus—a phenomenon that I interpret as atavistic. These highly divided fertile leaves are not uncommon; even the type at Paris contains a sheet with a 3-pinnate fertile leaf (Fig. 19g). As might be expected, intermediates exist between coenosoric and botryoid fertile leaves (Fig. 19f). Still, the most common type of fertile leaf in *P. serratifolia* is 2-pinnate (coenosoric) with relatively short pinnules (Fig. 19a,c).

In addition to its finely divided fertile leaf, *Polybotrya crassa* was distinguished by having an acroscopic auricle and several lobes at the pinna base. This condition represents nothing more than a part-fertile, part-sterile leaf; such transitional forms are commonly found in other species of subgenus *Soromanes* and frequently cause taxonomic confusion. Accordingly, *P. crassa* is here placed in synonymy.

Fée's citation of the type locality and collector ("Mexicana republica, Lagunetta (Galeotti). -V.S. in herb. Bory") seems to be the result of confusion. One of the labels on the type specimen reads (my translation): "Lagunetta, sent from Galeotti, October 1845." The word Lagunetta appears without mention of Mexico. Fée probably thought that Galeotti had collected the specimen in Mexico, the principal American country in which Galeotti collected (Morton 1971:63). Galeotti returned to Europe in 1840, where he sold many duplicates of his own and other collections. Morton (1971) observed: "Galeotti collected only in Mexico and a few specimens in Cuba but is often cited as the collector of plants from Brazil, Venezuela, and Colombia, but these plants were actually collected by Linden, and Galeotti was merely the distributor of the Linden plants." Presumably, Jean Jules Linden collected the type of *P. serratifolia*, which was later distributed by Galeotti. Although Linden collected in Cuba, Mexico, and Guatemala, his last and most profitable trip was to Venezuela and Colombia (1841–1844) where, based on other collections, this species is known to occur. *Polybotrya serratifolia* has not been collected in Mexico. I cannot find a town called "Lagunetta" in Mexico, but a town with that name is located in the state of Lara, Venezuela, and I suspect that is where Linden collected the type.

Specimens examined: TRINIDAD. *Prestoe 1491* (MO), *1492* (MO); heights of Aripo, *Broadway 9947* (GH, US), *9949* (F, NY, US), *Fay 859* (BM).

VENEZUELA. **Aragua:** Cordillera Interior, Cerro El Pauji, Topo El Pauji, al sur de El Consejo, *Steyermark & Stoddart 118051* (GH, VEN); cerca Tejerias, *Vareschi 7764* (VEN); Parque Nacional "H. Pittier," bosque de Rancho Grande, *Tschudi 167* (VEN); Colonia Tovar, *Fendler 235* (BM), *261* (GH, K, MO, NY, PH, US); Colonia Tovar, *Moritz 277* (BM). **Falcón:** Curimagua (Coro), *van Cotthem 1327* (UC); Sierra de San Luis, Montaña de Paraguariba, *van der Werff & Wingfield 3430* (MO). **Distrito Federal:** between El Junquito and Colonia Tovar, *Steyermark 91756* (GH, VEN); El Junquito, *Schnee 615* (VEN); off road Caracas–Colonia Tovar, in forest below Club Jundolandia, *Berry 948* (VEN). **Lara:** Lagunetta, *Galeotti s.n.* (P); Dtto. Morán, 8.7 mi SE of Sanare, Parque Nacional Yacambu, *A.R. Smith 1259* (PORT, UC); Dtto. Morán, *Rivero et al. 1608* (PORT); Dtto. Iribarren, Parque Terepaina, *Iriarte 52* (PORT); Dtto. Andres Elroy Blanco, 7 km de Sanare,

Rivero 513A (PORT); selva arriba de Sanare, *Aristeguieta 3963* (US, VEN); 2200 m sobre los baños de Río Claro, *A.R. Smith 4055*. **Mérida:** vertientes del Río Capaz, arriba de La Azulita, *Steyermark & Rabe 97133* (VEN); rich forest above Hacienda Agua Blanca, above La Azulita, *Steyermark 56114* (F, US). **Monoagas:** south-facing forested slopes above limestone bluffs, northeast of Guacharo, alt. 1300–1400 m, 11 April 1945, *Steyermark 61991* (F, US, VEN). **Portuguesa:** 15 km E of Chabasquen, 67 km NNW of Guanare, *Steyermark et al. 126675* (PORT), *126680* (UC, VEN). **Trujillo:** arriba de Escuque, entre Escuque y La Mesa de San Pedro, *Steyermark 104717* (MO, VEN); Dtto. Bocono, ca. 10 mi SW of Batatal on road to Bocono, Laguna de Aguas Negras, *A.R. Smith et al. 922* (PORT, UC); 2 km NW of Caserío Cerros de Guaramarcal, 42 km SE of Bocono, *Moran 3709* (F, MO, PORT, VEN). **Yaracuy:** El Amparo hacia Candelaria, a 7–10 km al Norte de Salom, *Steyermark et al. 106758* (NY, MO, PORT); Distrito Bruzual, Serranía de Aroa, 11–15 km NNE of Urachiche, 3 km NE of Caserío Buenos Aires, *Steyermark et al. 124749* (PORT, UC, VEN); Dtto. Bolívar, entre las Parchitas, Tierra Fria y Ojo de Agua, *Ortega & Smith 2491* (PORT), *2510* (PORT).

2. Polybotrya polybotryoides (Baker) Christ (Figs. 20 & 21, Map 2).

Polybotrya polybotryoides (Baker) Christ, Bull. Herb. Boissier, II. 1:70. 1901.

Acrostichum polybotryoides Baker, J. Bot. 207. 1881. TYPE: Colombia. Norte de Santander: Ocaña, on trees in the forest, 7000 ft., *Kalbreyer 1254* (holotype: K, color slide at MO!; photo GH!, MO!).

Acrostichum juglandifolium Baker, J. Bot. 207. 1881. *nom. illeg.*, *non* Kaulfuss, 1824. TYPE: Colombia. Antioquia: *Kalbreyer 1798* (holotype: K, color slide at MO!; photo GH!, MO!).

Polybotrya juglandifolia Christ, Bull. Herb. Boissier, II. 4:965. 1904. *nom. nov.* for *Acrostichum juglandifolium* Baker, *non* Kaulfuss, with same type.

Polybotrya juglandifolia Christ var. *lobata* Christ, Bull. Herb. Boissier, II. 6:168. 1906. TYPE: Costa Rica. Cartago: Río Navarro, Coll. Inst. Costaricensis no. 16769, *Wercklé s.n.* (P?).

Polybotrya kalbreyeri C. Chr., Index Filicum. 504. 1906. *nom. superfl.* for *Polybotrya juglandifolia* Christ; with the same type.

Polybotrya aucuparia Christ, Bull. Herb. Boissier, II. 6:166. 1906. TYPE: Costa Rica. Cartago: Valley of the Río Navarro, 1400 m, *Wercklé 16770* (P!; photos F!, NY!, UC!).

Stem 0.5–2.0 cm thick, hemiepiphytic; *scales* linear, mostly 9–15 mm long, 0.5–1.0 mm wide, ascending with spreading tips, lustrous, golden yellow when fresh, turning yellow brown to purple brown upon drying, margins denticulate. *Sterile leaves* up to 1.45 m long; *petioles* up to 45 cm long; *lamina* up to 1.0 m, 1-pinnate, but occasionally becoming pinnate-pinnatifid to 2-pinnate in transitional sterile-fertile leaves, subcoriaceous, dark green adaxially, pale green abaxially, nearly glabrous on both surfaces; *pinnae* up to 12 pairs, mostly 12–20(30) × 3–6(8) cm, lanceolate, the base round, cuneate or subtruncate, with the acroscopic side slightly prolonged, the margins entire, crenate or serrate, the apex acuminate; *veins* in pinnate groups 5–12 mm apart, the side branches ascending and anastomosing at acute angles with the adjacent ones (rarely, the veins fail to anastomose locally), the vein tips connected by a faint intramarginal connecting strand; *axes* nearly glabrous or with scattered hairs, these unicellular and colorless. *Fertile leaves* 2-pinnate, 12–28 cm broad; *pinnules* oblong to linear, 0.9–2(2.5) × 1–2 mm; *sori* coenosoric, continuously covering the abaxial surface of the pinnules; *sporangial stalks* paraphysate; *spores* mostly (45)50–65(68) microns long. $n = 41$.

Other illustrations: Ettingshausen, Farnkr. fig. 2. 1864 (as *P. kunzei*, portion of pinnae showing vein); Hooker, Icones Plant. 1877. pl. 1690 (as *Acrostichum polybotryoides*) and pl. 1691 (as *A. juglandifolium*); Rovirosa, Pterid. Sur. Mex. pl. 60. 1909 (as *A. coenopteris*); Smith, Flora of Chiapas, part II, fig. 71. 1981 (as *P. aucuparia*); Stolze, Fieldiana Bot. II. fig. 60d, 1981 (portion of pinna with venation, as *P. aucuparia*).

Polybotrya polybotryoides grows in wet, shaded, tropical forests from sea level to 1400 (1850)m. It has the largest range of any species in subgenus *Soromanes*, even occurring on Cocos Island (Map 2). Gómez (1976) reported this species from Nicaragua, but I have not seen a specimen from that country.

The shape of the leaf apex varies clinally from southern Mexico to Peru (Fig. 21). From southern Mexico to Costa Rica, the apex is pinnatifid, hav-

FIGURE 20. *Polybotrya polybotryoides* (Baker) Christ. a. northern apex form, Guatemala; b. sterile leaf with intermediate apex form, Panama; c. southern apex form, Ecuador; d. fertile leaf; e. sterile pinna; f. stem scales. a: *Steyermark 37320* (F). b: *Croat 12143* (MO). c,d: *Moran 3569* (F). e,f: *Moran 2178* (CR).

ing two to four basal lobes; this apex does not resemble the lateral pinnae. South of Costa Rica, the apex resembles the lateral pinnae because it has only one or two basal lobes with the remainder of the apex relatively narrow and the margins entire to crenate. Since apex shape varies clinally and no other characters correlate with it, I interpret the two extreme shapes as geographic variations of the same species and do not believe that these should be named. Plants having an intermediate apex shape do not appear to be hybrids, since they do not have aborted spores. In South America, the nearly conform apex of *P. polybotryoides* is taxonomically useful because the three other species of subgenus *Soromanes*, which might possibly be confused with this species, have strongly and evenly pinnatifid apices. The subconform apex in southern populations of *P. polybotryoides* is derived within the genus, as evidenced by comparison to all other species of *Polybotrya* and to all other genera of dryopteroid ferns.

Polybotrya polybotryoides is most like *P. suberecta*. Another morphological character separating these two, besides apex shape, is the submarginal connecting vein present in *P. polybotryoides* (Fig. 20e) but only partially formed in *P. suberecta* (Fig. 22d). Unfortunately, the connecting vein is faint and difficult to see because of the thick lamina and, in some specimens, margins that have become revolute upon drying and thereby hide the region just inside the margin. The connecting strand is best seen with magnification on the abaxial surface of the pinna or with the unaided eye and the pinna held up to strong light.

Specimens examined: MEXICO. **Chiapas:** Tumbala, *Rovirosa 972* (GH, PH); Finca Mexiquito, *Purpus 6761* (BM, F, GH, MO, NY, UC, US), *7245* (BM, GH, US); 18–20 km N of Ocozocoautla de Espinoza, along road to Mal Paso, *Breedlove & Smith 21886* (MICH, NY, UC).

BELIZE. **Cayo:** Hwy 28.5 mi S of Belmopan, *Croat 24566* (CR, MO); Toledo district, Maya Mts., between Río Caraval and Union Camp, *Boutin & Schlosser 5902* (MO).

GUATEMALA. **Alta Verapaz:** 7 mi up the road to Oxec along road off Hwy. 7E between Tucuru and El Estor ca. 6 km NE of Panzos, *Croat 41637* (CR, MO). **Izabal:** along Río Bonita, Cerro San Gil, *Steyermark 41698a* (F, US); Cerro San Gil, *Steyermark 41870* (F). **Quezaltenango:** near Calahuache, *Standley 67135* (F); Finca Pireneos, below Santa María de Jesús, *Standley 68203* (F). **San Marcos:** above Finca El Porvenir, Volcán Tajumulco, up Loma Bandera Shac, *Steyermark 37320* (F).

HONDURAS. **Atlántida:** Lancetilla Valley, near Tela, *Standley 53955* (F, US); Montaña La Manga, 30 km SE de La Ceiba, *Nelson et al. 3296* (MO); Cordillera Nombre de Dios, *Gómez 7027* (CR). **Comayagua:** Quebrada Potrero, Cerro Azul de Meambar, *Gómez 6914* (CR). **Cortés:** mountains on N side of Lake Yojoa, *Morton 7629* (US).

COSTA RICA. **Cartago:** Valley of the Río Navarro, 1400 m, *Wercklé 16770* (P, photos F, NY, UC); along Camino Raiz de Hule, SE of Plantanillo, *Croat 36800* (CR, MO); Raiz de Hule, Moravia de Chirripó, *Ocampo 727* (CR); Chitaría, forest near old jailhouse, *Moran 2170, 2171, 2173, 2176, 2178* (CR, F, MO, NY); Chitaría, *Valerio 329* (US), *33133* (CR); Finca Navarro, *Maxon 639* (NY). **Cocos Island:** Wafer Bay, *Gómez 3324* (CR, F, US); Wafer Valley, *Pittier 16232* (CR, US); Wafer Bay river valley, *Holdridge 5153* (GH), *Klawe 1545* (US); trail between Chatham and Wafer bays, *Gómez 18064* (CR); Chatham Bay, *Jiménez M. 3209, 3210* (CR, F, GH, MICH); Chatham Bay, *Fournier 357* (NY). **Puntarenas:** Osa Peninsula, on ridge 9.5 km W of Rincon de Osa, *Mickel 2742* (NY); above San Vito at Finca Wilson, NE of home, *Evans & Bowers 3152* (MO); vicinity of biological field station at Finca Wilson, 5 km S of San Vito de Java, *Mickel 3180* (NY). **San José:** Carrillo, *Brade 372* (UC).

PANAMA. **Coclé:** Continental divide on road to Coclesito, *Hammel 3503* (CR). **Darién:** El Llano–Cartí road, *Churchill & de Nevers 4993* (MO); Serranía de Pirre, along ascent of Serranía de Pirre above Cana Gold Mine between Río Cana and Río Escucha Ruido, *Croat 37757* (MO), *37794* (MO). **Panamá:** El Llano–Cartí road, 13.7 km N of Pan-American Highway, *Folsom 3590* (MO); Cerro Campana, ca. 10 km SW of Capira, trail to summit, *Mori & Kallunki 3574* (MO, NY); 1 mi upstream from Frizzel's Finca Indio, on slopes of Cerro Jefe, *Foster & Kennedy 1814* (F, MO); Cerro Jefe, *Webster et al. 16467* (UC); along road to Cerro Campana, *Croat 14687* (F, MO, NY); trail to Cerro Campana, *Kirkbride & Hayden 274* (MO, NY); Cerro Campana, FSU Field Station, *Kennedy et al. 2074* (MO); cloud forest on Cerro Campana above Su Lin Motel, *Croat 14742* (MO); Cerro Campana, above Su Lin Motel, *Croat 4266* (MO); Cerro Campana, near FSU building, *Croat 12114* (F, MO), *12143* (MO, US), *14786* (MO); 8–12 km N of El Llano, along new El Llano–Cartí road, *Nee et al. 8768* (MO); Cerro Campana, lower slopes above FSU cabin, *Croat 22789* (MO); Cerro Campana along trail to summit, *Croat 17161* (MO, US); high point of ridges S of Ipeti, 5–6 hr walk from Chocó village, Serranía de Maje, *Knapp et al. 4542* (MO); along trail to top of Cerro Campana, SW slope from road, *Nee & Stockwell 11610* (MO); Cerro Campana, *Armond 298* (MO). **Veraguas:** 5 mi NW of Santa Fé, slope above Río Primero Brazo, below Escuela Agricola Alta Piedra, *Croat 23244* (MO), *Liesner 820* (MO); Valley of Río Dos Bocas along road between Escuela Agricola Alto Piedra and Calovebora, 15.6 km NW of Santa Fé, *Croat 27648* (MO); 0.6 mi beyond Escuela

Agricola Alto Piedra, *Croat & Folsom 34051* (MO); vicinity of Escuela Agricultura Alto Piedra near Santa Fé along trail to top of Cerro Tute, *Antonio 4019* (MO); ridge of Cordillera de Tute, trail to Cerro Tute, above Escuela Agricola Alto de Piedra, just W of Santa Fé, *Knapp & Dressler 5461* (MO).

COLOMBIA. **Antioquia:** *Kalbreyer 1798* (K, color slide at MO; photo GH, MO); vic. Planta Provedencia, 28 km SW of Zaragoza, *Alverson et al. 342* (MO, US); cerca de Porcesito en el valle de Río Medellín, *Hodge 6780* (GH); Barbosa, *Henri-Stanislas 1709* (US). **Chocó:** Trail to Miniquía E of Puerto Mutis, *Lellinger & de la Sota 39* (US); Río Mutatá ca. 3 km above junction with Río El Valle, NW of Alto del Buey, *Lellinger & de la Sota 190* (US). **Norte de Santander:** Ocaña, on trees in the forest, alt. 7000 ft., *Kalbreyer 1254* (K, color slide at MO; photo GH, MO).

ECUADOR. **Bolívar:** Limón, estrivaciones inferiores de la Cordillera Occidental, *Acosta Solis 6358* (F). **Napo:** 73 km al noreste de Baeza, Cascada de San Rafael, *Moran 3593* (Q, QCA), *Foster 85-162* (UC); camino Baeza–Tena, 15 km al norte de Tena, *Moran 3530* (Q, QCA). **Morona-Santiago:** Cordillera de Cutucu, western slopes, trail from Logrono to Yaupi, *Madison et al. 3356* (GH). **Pastaza:** 6.5 km W of Mera, *Moran 3590* (F, Q, QCA). **Pichincha:** Hotel Tinalandia, bosque primario al lado norte del Río Toachi, *Moran 3562* (Q, QCA). **Tungurahua:** 25 km al este de Baños, detras el pueblo Río Negro, *Moran 3569* (F, Q, QCA).

PERU. **Huánuco:** SW slope of Río Lulla Pichis watershed, ascent of Cerros del Sira, *Dudley 13290D* (GH). **Pasco:** Prov. Oxapampa, Abra los Mellizos, 4–8 km from Enanas, *Skog et al. 5036* (US).

FIGURE 21. Clinal variation in apex shape of *Polybotrya polybotryoides* (Baker) Christ. Plants from the northern portions of the range have deeply and evenly pinnatifid apices. Southward, this shape gradually changes into a subconform apex. Intermediates are found primarily in Costa Rica and Panama.

3. Polybotrya suberecta (Baker) C. Chr. (Fig. 22, Map 1).

Polybotrya suberecta (Baker) C. Chr., Index Filicum 506. 1906.

Acrostichum suberectum Baker, J. Bot. 207. 1881. TYPE: Colombia. Antioquia: 4000–4500 ft., *Kalbreyer 1877* (holotype: K, color slide at MO!; photo GH!, US!).

Acrostichum hackelianum Sodiro, Anal. Univ. Quito XII (78):21. 1895. (Crypt. Vasc. Quit. 491. 1893.) TYPE: Ecuador. Pichincha: banks of the Río Pilaton, *Sodiro s.n.* (holotype: Q!).

Stem 1–2 cm thick, hemiepiphytic; *scales* dark brown, narrow, linear, 0.2–0.4(1.0) × 8–15 mm, stiff to spreading. *Sterile leaves* up to 1.6 m long; *petioles* about ½ to ¾ the length of the lamina, scaly at base, becoming less so distally; *lamina* 1-pinnate, mostly 0.5–1.0(1.2) m long, lanceolate; *pinnae* oblong-lanceolate, (10)15–21(25) × (3)4–5(6.5) cm, 6–13 free pairs, glabrous to densely pubescent beneath, the hairs uncinate, multicellular, reddish or clear, 0.1–0.6 mm long, the margins entire, or (more rarely) shallowly and inconspicuously serrate, the base cuneate to broadly rounded, the apex acuminate; *veins* anastomosing, the tips sporadically uniting to form a discontinuous, submarginal connecting strand; *axes* with a few narrow, scattered scales, usually glabrous, rarely pubescent by uncinate hairs, or rarely by short (less than 0.2 mm), subulate, clear hairs. *Fertile leaves* 2-pinnate to 2-pinnate-pinnatifid, 10–30 cm wide, pectinate; moderately scaly, the scales appressed, linear; *pinnules* linear, 25–55 × 1–3 mm; *sori* coenosoric, continuously covering the abaxial surface of the pinnule; *sporangial stalks* paraphysate; *spores* (43) 46–55(58) microns long.

Other illustrations: Hooker, Icones Plant. 17, pl. 1692. 1877 (as *Acrostichum*).

Polybotrya suberecta grows in montane forests from 600 to 1800 m elevation. Most of the specimens are from the western slopes of the Andes (Map 1). These locations correspond to my field experience in Ecuador, where this species was common on the western side of the Andes but absent from the eastern side.

The range of this species overlaps with *P. polybotryoides*, a similar species. The two species are most easily distinguished by the shape of the leaf apex; *P. polybotryoides* has a subconform apex in Colombia and Ecuador, but *P. suberecta* has an evenly tapering, pinnatifid apex. Other distinguishing characters of *P. suberecta* are the uncinate hairs that occur in some specimens (Fig. 22a) and the discontinuous, submarginal connecting vein (Fig. 22d). *Polybotrya serratifolia* also resembles *P. suberecta* but differs by its wide, flaccid stem scales and a distribution that is restricted to high altitude forests in Venezuela and Trinidad (Map 1). *Polybotrya suberecta* looks very much like *P. andina*—a species with which it grows in the western Andes of Ecuador. See *P. andina* for comparison.

Specimens examined: COLOMBIA. **Antioquia:** 4000–4500 ft., *Kalbreyer 1877* (K, color slide at MO; photo GH, US). **Chocó:** hills above Río Capa and Río Mumba, up river from Lloro, *Juncosa 1467* (MO, COL); NW side of Alto del Buey, *Lellinger & de la Sota 248* (COL, LPB, US); 0.3 km E of the Ciudad Bolívar–Quibdó road, across the suspension bridge at km 141, *Lellinger & de la Sota 894* (COL, US). **Cundinamarca:** Ojo de Agua, S side of Río Guavio, 32 km E of Gachala, *Grant 10556* (US). **Magdalena:** below Valparaiso, *H.H. Smith 983* (F, GH, NY); "Cincinnati," lower slopes of Mt. San Lorenzo, near Sta. Marta, 1300 m, *Seifriz 24* (US). **Santander:** along highway between Pamplona and Bucaramanga, Munic. Tona, Corregimento Corcova, Vereda la Marina, *Croat 56510* (MO, UC).

ECUADOR. **Los Ríos:** Patricia Pilar, *Dodson 7380* (COL, MO, US), *Dodson et al. 8679* (MO, US). **Pichincha:** banks of the Río Pilaton, *Sodiro s.n.* (Q); 2.5 km E of Cornejo Astorga, *Moran 3546.5* (F, GH, Q, QCA); 3 km from El Paraiso, road El Paraiso–Saguangal, *Øllgaard et al. 37823* (AAU, Q, QCA); 3 km from La Armenia, road Gualea–La Armenia, *Øllgaard et al. 37859* (AAU); about 40 km WNW of Quito, 3.5 km N of Mindo, *Moran 3565* (F, GH, Q, QCA); Tinalandia Resort, N side of Río Toachi, about 25 km E of Sto. Domingo, *Moran 3561* (F, GH, Q, QCA); ca. 2 km N of Mindo, Hacienda San Vicente, *Foster 85-37* (UC).

PERU. **Junín:** Prov. Tarma, Chanchamayo, *Esposto 10928* (USM).

4. Polybotrya andina C. Chr. (Fig. 23, Map 2).

Polybotrya andina C. Chr., Index Filicum 7. 1905. *nom. nov.* for *Acrostichum insigne* Baker, *non* Fée 1872–73, with same type.

Acrostichum insigne Baker, J. Bot. 167. 1877. *nom. illeg.*, *non* Fée 1872–73. TYPE: Ecuador. Pichincha: "Andes of Quito," *Sodiro* (holotype: K, photo GH!, US!; isotypes: AAU!, GH!, Q!, UC!).

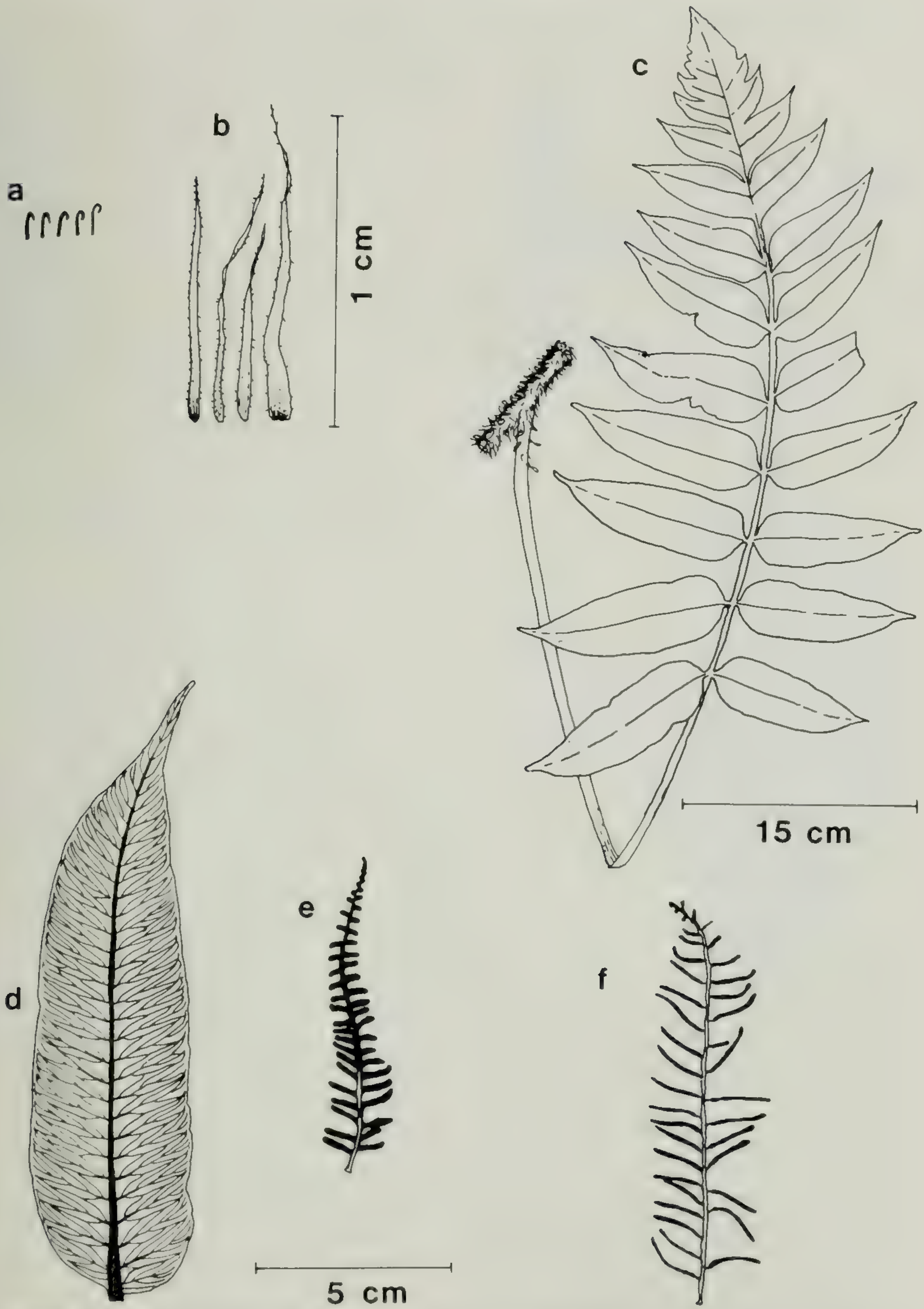

FIGURE 22. *Polybotrya suberecta* (Baker) C. Chr. a. uncinate hairs from abaxial leaf surface; b. stem scales; c. sterile leaf; d. sterile pinna; e,f. fertile pinnae. a: *Øllgaard et al. 37823* (AAU). b–d: *Moran 3546.5* (F). e: *Smith 983* (NY). f: *Dodson 7380* (US).

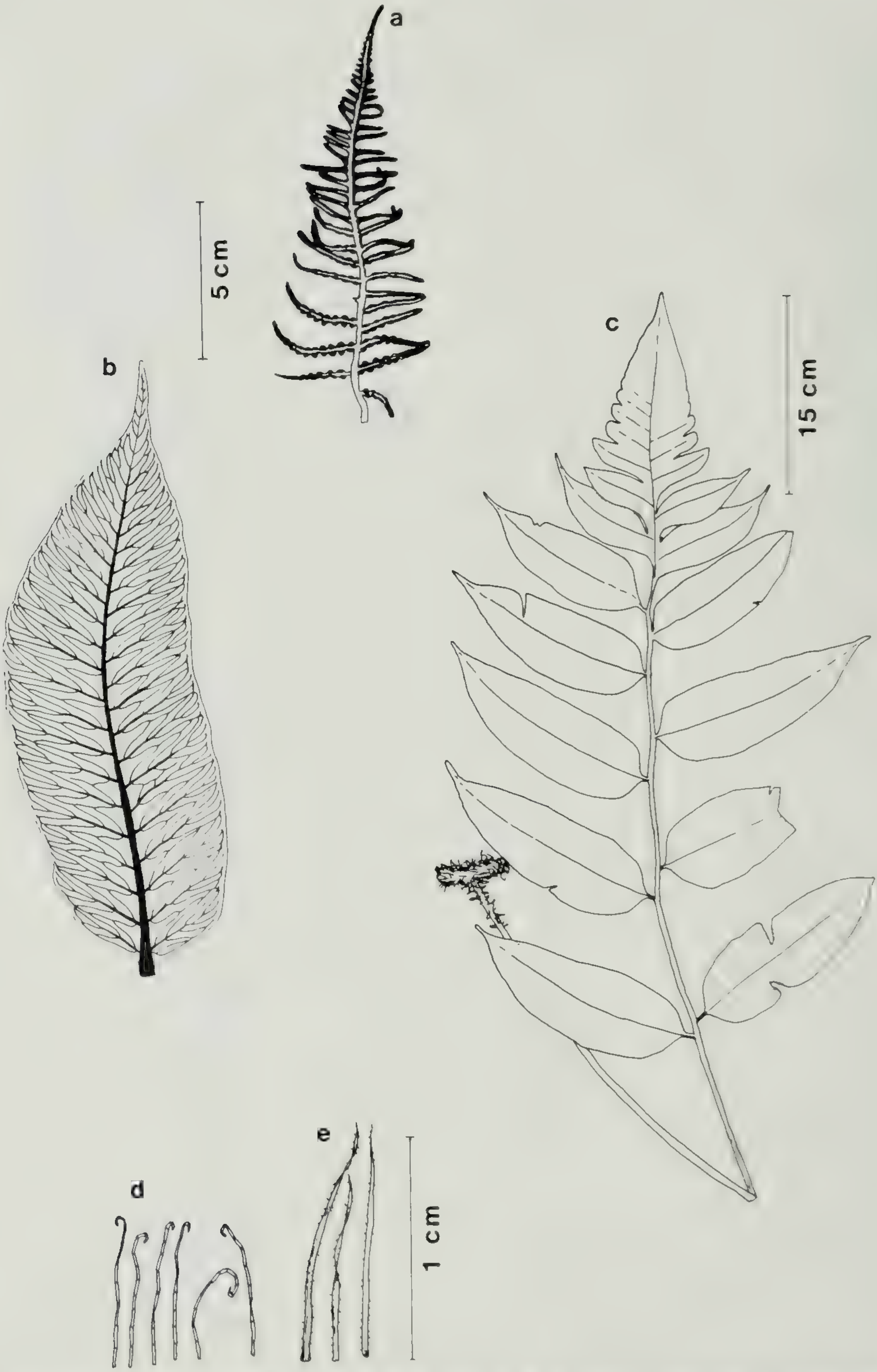

FIGURE 23. *Polybotrya andina* C. Chr. a. fertile pinna; b. sterile pinna; c. sterile leaf; d. multicellular uncinate hairs from abaxial surface of the leaf; e. stem scales. a: *Sodiro s.n.* (AAU). b–e: *Moran 3563* (F).

Stem 1–1.5 cm thick, hemiepiphytic; *scales* mostly 8–13 mm long, dark castaneous, shiny or dull, opaque, margins denticulate. *Sterile leaf* up to 1.0 m long; *petiole* up to 30 cm long, ¾ to as long as the lamina, scaly at base, becoming less so upwards; *lamina* mostly 60–80 × 30–50 cm, deltate or broadly ovate-lanceolate, subcoriaceous, glabrous above, below densely pubescent with spreading, tawny, uncinate, 4-to-10-celled hairs, these 0.5–1.2 mm long; *pinnae* 17–33 × 5.7–10 cm, mostly less than 3.5 times as long as broad, 4–7 pairs below the pinnatifid apex, margins entire, base cuneate-rounded, petiolulate, gradually becoming sessile distally; *veins* anastomosing, the tips uniting discontinuously; *axes* pubescent, the hairs like those on the lamina. *Fertile leaves* slightly smaller, 40–80 × 20–32 cm, pubescent with hairs like those of the sterile lamina; *pinnae* pectinate; *pinnules* proximally lobulate, becoming entire apically, 3–6 mm wide; *sori* coenosoric, covering most of the abaxial surface of the pinnule; spore length unknown.

Sodiro (1897) noted that this species "grows in the tropical and subtropical region up to 1200 m in the forests around Sto. Domingo de los Colorados and in the Nanegal and Mindo valleys" (translation mine). This species is very rare and restricted in range and has been collected only twice from the western cordillera of Ecuador west of Quito (Map 2). I saw only three plants at the Tinalandia site. *Polybotrya suberecta* and *P. polybotryoides* also occurred at this locality and were more abundant.

This species is most closely related to *P. suberecta*, from which it differs by its longer and wider pinnae, fewer (4–7) free pinnae pairs below the apex, and spreading, multicellular, tawny hairs on the abaxial surface (Fig. 23d). Pubescent plants of *P. suberecta* occur in the region of Ecuador where *P. andina* grows. Within this region, the hairs of both species are uncinate, but in *P. suberecta* they are much shorter (0.1–0.3 mm), 1- or 2-celled, erect, and easily overlooked by the naked eye (Fig. 22a). Only these two species of *Polybotrya* have uncinate hairs. Because the fertile leaf of *P. andina*, known only from Sodiro's type collection, had very few spores, I could not make an adequate measurement of spore length.

Specimens examined: Ecuador. **Pichincha:** Hotel Tinalandia, casi 25 km al este de Sto. Domingo de los Colorados, bosque primario arriba la montaña al lado norte del Río Toachi, 1000 m, *Moran 3563* (F, Q, QCA); "Andes of Quito," *Sodiro s.n.* (K, photo GH, US; AAU, GH, Q, UC).

POLYBOTRYA subgenus SORBIFOLIA

Moran, *subgen. nov.*

Type species: *P. sorbifolia* Kuhn, Linnaea 34:64. 1869.

Folia 1-pinnata, pinnae lineares vel lanceolatae, 6–10 sexies vel decies longiores quam latiores, apice longiacuminato; venae sibi parallelae pinnatae, 3–5 in quoque turmae, liberae.

Stem terrestrial and short-creeping (2 spp.) or hemiepiphytic and long-creeping (1 sp.). *Sterile leaves* 1-pinnate; pinnae linear to lanceolate, 6–10 times as long as broad, apices long-acuminate; veins in pinnate groups of 3–5, strongly ascending, free all the way to the margin. *Fertile leaves* pectinate or more rarely, moniliform.

5. Polybotrya sorbifolia Kuhn (Fig. 24, Map 3).

Polybotrya sorbifolia Kuhn, Linnaea 36:64. 1869. Based on var. *salicifolium* Hooker and with same type.

Acrostichum caenopteris Hooker var. *salicifolium* Hooker, Species Filicum 5:257. 1864. Type: Brazil. Pernambuco: Serra do Araripe, *Gardner 1901* (holotype: K, photo GH!; fragment NY!).

Polybotrya salicifolia Lellinger, Amer. Fern J. 62:54. 1972. Type: Colombia. Santander: vicinity of Puerto Berrio, between Carare and Magdalena River, 100–700 m, 8 June 1935, *Haught 1757* (holotype: US!; isotype: BM!).

Stem terrestrial, 1–2.5 cm thick; *stem scales* shiny brown, linear, 0.4–1 × 10–20 mm, membranaceous, spreading, the margins denticulate. *Sterile leaves* up to 1.3 m; *petiole* 15–50 cm long; *lamina* lanceolate to oblanceolate, 0.3–1.5 × 0.15–0.50 m, chartaceous, with 12–18 pinnae pairs, the apex abruptly acuminate, its lowermost lobes decurrent; *pinnae* lanceolate-acuminate, (7.3)10–22(25.5) × (0.7)1–3(3.5) cm, the base truncate on its acroscopic side, cuneate on the basiscopic side, the margins entire, crenate, usually serrate at the apex, the abaxial surface glabrous or glandular, the glands scattered, round, whitish to reddish, sessile glands; *veins* slender, sharply ascending, long parallel, usually oblique to the costa, the tips free; *axes* with a few scattered, appressed scales. *Fertile leaves* lanceolate, 0.3–1.3 × 15–40 m, pinnate-pinnatifid; *pinnae* linear, 4–15 × 0.7–1.0 cm, moniliform because of the round to oblong pinnules, these 1–3 mm wide;

sori coenosoric, completely covering the abaxial surface of the pinnules; *sporangial stalks* paraphysate; *spores* mostly 40–47 microns long.

Other illustrations: Murillo, Cat. Illustrado de las Plantas de Cundinamarca, 2:103. 1966 (as *P. serratifolia*); Vareschi, Flora Venez., Helechos, vol. I, tab. 73. 1968 (as *P. serratifolia*); Brade, Bradea 1(9):62, fig. 3. 1971 (as *P. serratifolia*); Lellinger, Amer. Fern J. 62, figs. 3, 4, 10. 1972 (as *P. salicifolia*).

The distribution of *P. sorbifolia* is spotty but extensive (Map 3). This species looks like *P. fractiserialis*; see that species for comparison. Unlike all other species in the genus, both *P. sorbifolia* and *P. fractiserialis* are terrestrial—*never* climbing—and it is doubtful that they could climb because their stems are only short-creeping. Both species grow in shaded, rocky habitats along streambanks, from 0–1200 m. I collected *P. sorbifolia* in Costa Rica at the El Rodeo site. It is common at this locality, growing on talus along a stream in the bottom of a humid, limestone ravine that is surrounded by dry uplands.

Unfortunately, the specific epithet "*salicifolia*" cannot be used for this species even though its pinnae bear a strong resemblance to leaves of certain *Salix* species, most notably *S. nigra* and *S. amygdaloides*. This resemblance was noted by Hooker (1864) and Lellinger (1972).

Specimens examined: COSTA RICA. **San José:** Alajuelita, *Alfaro 8073* (US); El Rodeo, *Moran 3145* (CR, F, GH, MO, PORT), *Knight s.n.* (US), *Gómez 7122* (CR), *Hunnewell 16514* (MICH).

VENEZUELA. **Aragua:** Parque Nacional "H. Pittier," Rancho Grande, *Tschudi 162* (VEN), *Steyermark et al. 95827a* (US). **Portuguesa:** Dtto. Araure, Fila San José, al oeste de Sta. Lucía, *Ortega & Grimann 2707* (PORT). **Yaracuy:** "La Enjalma" al sur de Chivacoa, *Vareschi & Pannier 2636* (US, VEN).

COLOMBIA. **Boyaca:** valle del Río Cusiana, entre Pajarito y Guazul, *Murillo 1457* (COL), *1491* (COL). **Cundinamarca:** entre Nilo y la quebrada de Agua de Diosito, *Murillo et al. 289* (COL, US). **Magdalena:** Santa Marta, near Jiracasaca, *H.H. Smith 1052* (F, GH, L, MICH, MO, NY, PH, US). **Meta:** along Cono Rosa Blanca, a small stream outside of Villavicencio, *Kirkbride 404* (MO, NY). **Santander:** vicinity of Puerto Berrio, between Carare and Magdalena River, *Haught 1757* (BM, US).

BRAZIL. **Goiás:** Serra Dourada, 17 km (straight line) S of Goiás Velho, 6 km NE of Mossamedes, *Anderson 10152* (NY). **Pará:** Serra dos Carajás, Serra Norte, near waterfall near AMAZ Exploration Camp, *Silva et al. BG 526* (AAU, F, GH, MICH, NY, UC). **Pernambuco:** Serra de Araripe, *Gardner 1901* (NY, photo of K specimen at GH). **Roraima:** Indian trail from Surucucu to Uaica, Maita Mts. *Prance et al. 10466* (NY).

6. Polybotrya fractiserialis (Baker) J. Smith (Fig. 25, Map 3).

Polybotrya fractiserialis (Baker) J. Smith, Hist. Filicum 133. 1875.

Acrostichum fractiseriale Baker, Synopsis Filicum 414. 1868. TYPE: Peru. San Martín: "in sylvis montis campana, terrestre," Dec. 1855, *Spruce 4337* (holotype: K, color slide at MO!; photo GH!, US!).

Acrostichum plumbicaule Baker, Synopsis Filicum 413. 1868. TYPE: Peru. San Martín: Terapoto, Ad rupes secus rivularum, Aug. 1855, *Spruce 4090* (lectotype: K, photo GH!, photo and fragment P!, US!).

Polybotrya plumbicaulis (Baker) J. Smith, Hist. Filicum 133. 1875.

Stem terrestrial, 1–1.5 cm thick, short-creeping with internodes 1–3 cm long, apex scaly, behind the apex usually naked or only sparsely scaly; *scales* dull brown, opaque, 0.3–0.9 × 8–17 mm, ascending, margins entire to more rarely denticulate. *Sterile leaves* to 1.4 m tall; *petiole* about equaling the lamina, stramineous to lead-gray; *lamina* slightly reduced or broadest at the base, chartaceous to subcoriaceous, apex with one or two major basal lobes, merely crenate-lobulate above; *pinnae* mostly 9–15 pairs, linear to oblong, (11)15–25(28) × (2.1)2.5–4.0(4.5) cm, margins serrate, especially towards the acuminate apex, base rounded to cuneate, with the acroscopic margin usually more oblique; *veins* numerous, fine, and in closely parallel pinnate groups, occasionally with a simple vein springing directly from the costa; *axes* usually glabrous or with fine, subulate, 0.1–0.2 mm hairs. *Fertile leaves* erect, 2-pinnate, commonly taller than the sterile, to 1.5 m long; *pinnae* linear, mostly 7–12(17) × 5–10(15) cm; *pinnules* round, oblong, or linear, 1–3 mm wide; *sori* coenosoric, completely covering the abaxial surface of the pinnule; *sporangial stalks* paraphysate, often with a bulbous glandular cell at base of the paraphysis; *spores* (48)52–56(60) microns long.

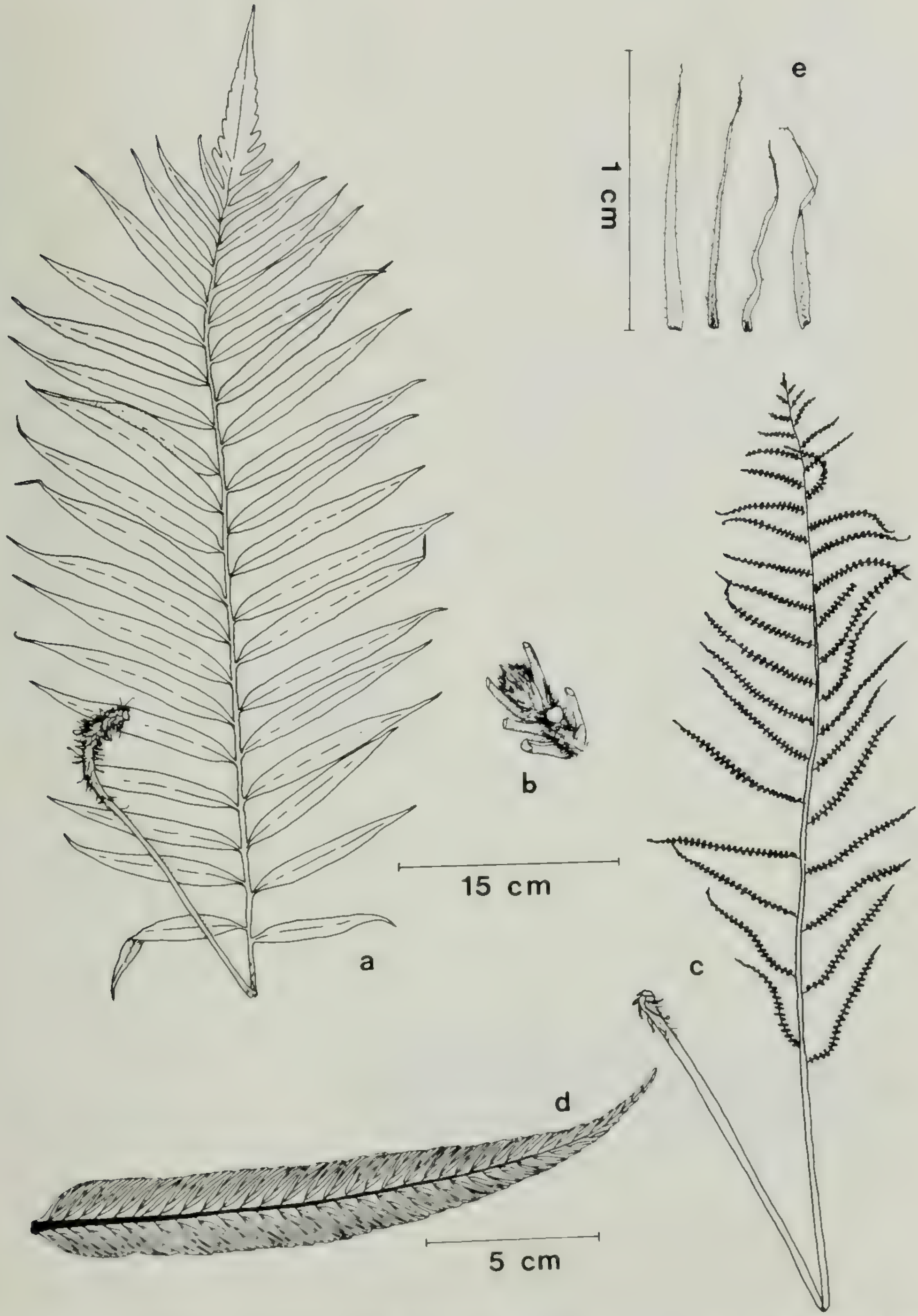

FIGURE 24. *Polybotrya sorbifolia* Kuhn. a. sterile leaf; b. stem; c. fertile leaf; d. sterile pinna; e. stem scales. a–e: *Moran 3145* (F).

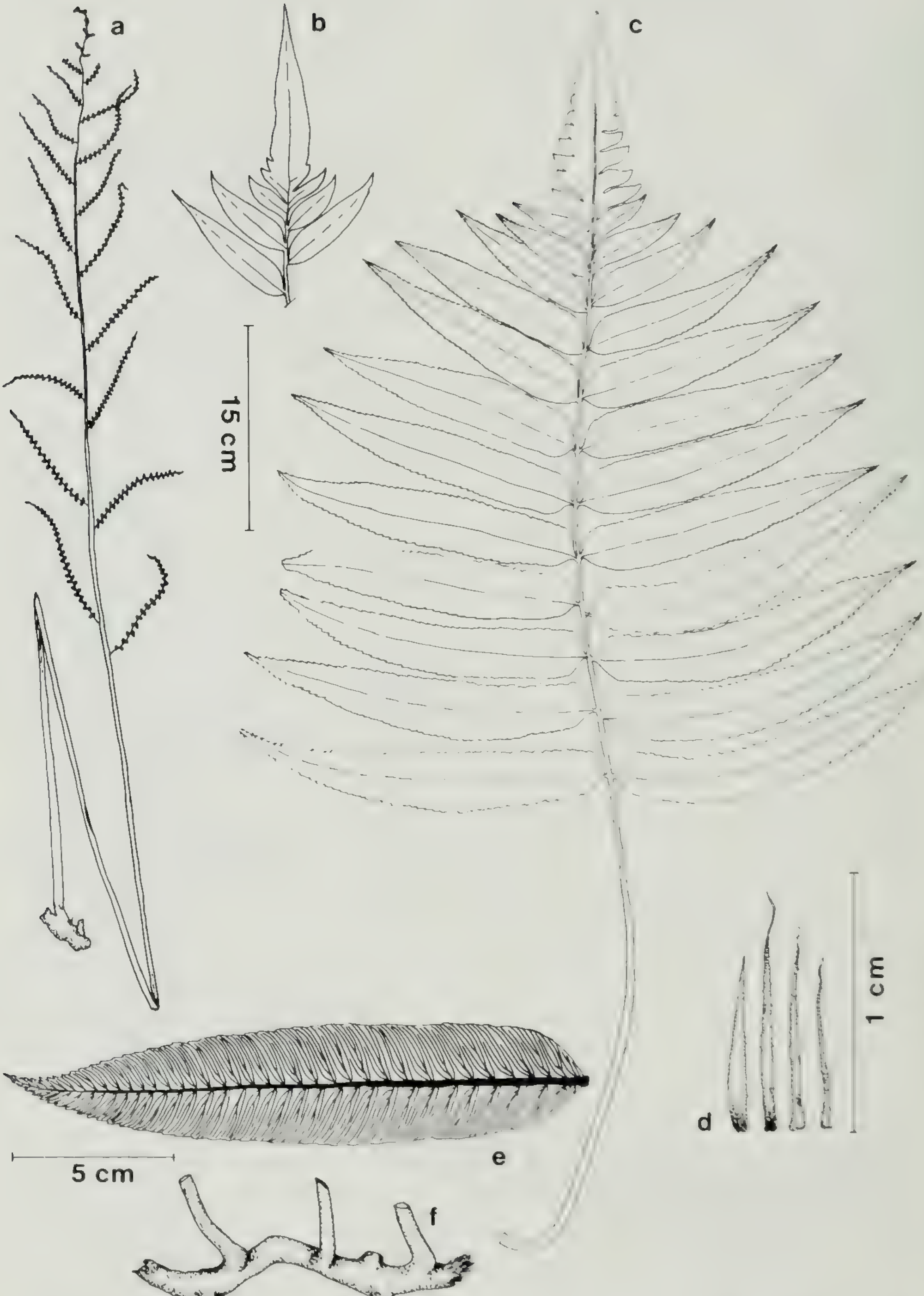

FIGURE 25. *Polybotrya fractiserialis* (Baker) J. Smith. a. fertile leaf; b. apex of sterile leaf; c. sterile leaf; d. stem scales; e. sterile pinna; f. stem. a: *C. Schunke 666* (F). b,d,e: *Moran 3536* (F). c: *Gonggrijp & Stahel 3300* (MO). f: *Tryon & Tryon 5221* (GH).

Other illustrations: Brade, Bradea 1(9):62, fig. 4. 1971 (as *P. polybotryoides*).

This species, like *P. sorbifolia*, is terrestrial and grows in wooded talus slopes, usually along rocky streamsides. The altitudinal range of *P. fractiserialis* is from 200–1500 m, but about 80 percent of the collections come from the 400–800 m range. Although principally a forest species, I have seen vigorous fertile plants growing along sunny streamsides in Ecuador, an observation which suggests that this species has more tolerance to higher light conditions than its cogenerics.

The range of *P. fractiserialis* occupies two discontinuous regions: 1) the Andes from Bolivia to Ecuador, and 2) the Guianas (Map 3). A distance of 900 km separates the northernmost population in Ecuador from the westernmost population in British Guiana. All populations of this species occur on the eastern side of the Andes. Their absence from the western side is probably due to the extreme dryness that characterizes that side of the Andes south of the equator.

Polybotrya fractiserialis and *P. sorbifolia* look very much alike and can be easily confused. Several characters, however, distinguish the two. The easiest feature to recognize is the shape of the medial pinnae: those of *P. fractiserialis* are relatively shorter and broader than those of *P. sorbifolia* (see key and descriptions); this stoutness is accentuated just below the apex (Fig. 25). The apex of *P. sorbifolia* is another difference; it has more numerous, decurrent, narrower pinnae (Fig. 24). Usually, the veins of *P. sorbifolia* are at a more oblique angle to the costa than those of *P. fractiserialis*. Another difference, albeit more recondite, is found in the sporangial stalks of *P. fractiserialis*, which have a lightbulb-shaped gland at the base of the paraphysis (Fig. 11f,g); *P. sorbifolia* lacks such a gland (Fig. 11b). In fact, no other species of *Polybotrya* has a glandular cell on the paraphysis or elsewhere on the sporangium. *Polybotrya sorbifolia*, however, has round, sessile glands on the lamina; such glands are lacking on *P. fractiserialis*.

Spore size is yet another diffence: *P. fractiserialis* has much larger spores than *P. sorbifolia*. This difference suggests that *P. fractiserialis* may be a polyploid, but chromosome counts are still wanting for the two species. Polyploidy has not yet been documented cytologically in *Polybotrya*.

Polybotrya fractiserialis and *P. plumbicaulis* were described at the same time, in the same publication, and were distinguished on the basis of leaf size, number of pinnae pairs, and two versus three or four veinlets in each pinnate group. These characters, however, intergrade completely even on leaves from a single plant. I chose the name *P. fractiserialis*, rather than the simultaneously published name *P. plumbicaulis*, because it was used by Posthumus (1928) in his treatment of Surinam ferns.

Specimens examined: FRENCH GUIANA. **Guyane:** Cayenne, 1847, *Leprieur s.n.* (P). **Inini:** Cocao, La Comte Riv., 1847, *Leprieur s.n.* (P); Tumuc Aumac, Haut Itany, *Hoock s.n.* (P); ca. 45 km SE of Saul, *Granville 3674* (CAY, Z); region de Paul Isnard, Montagne Lucifer, *Granville 5219* (CAY, Z); Saul, Monts du Fumée, *Granville 5121* (CAY, Z).

SURINAM. 3 km S of Juliana Top, 12 km N of Lucie Riv., *Maguire et al. 54384* (MO, NY), *Irwin et al. 54669* (NY), *54784* (F, MO, NY); Brownsberg, *Gonggrijp & Stahel 3300* (MO, US).

GUYANA. **Essequibo:** Southern Pakaraima Mts., Kopinang Falls, *Maguire et al. 46068-A* (NY).

ECUADOR. **Napo:** casi 10 km SE de Tena, 3 km E de Puerto Nuevo por camino a Puerto Misahuallí, *Moran 3536* (F, GH, MO, Q, QCA, US). **Pastaza:** Río Capihuari, tributary of Río Pastaza, *Øllgaard et al. 35124* (AAU).

PERU. **Amazonas:** Prov. de Bagua, Valley of Río Marañon above Cascadas de Mayasi near Campamento Sta. Montenegro (kms. 280–284 of Marañon rd.), *Wurdack 1854* (US). **Cuzco:** Prov. Paucartambo, *Vargas 11280* (GH). **Huánuco:** Prov. Huánuco, Tingo María, *Tryon & Tryon 5221* (GH); Tingo María, *Allard 20661* (US), *22305* (GH, US), *22526* (US); Previsto, antes de Aguaitia, *Aguilar 947* (USM); Prov. Leonicio Prado, Distrito Rupa Rupa, al este de Tingo María, cerca al Cerro Quemado, *J. Schunke 10173* (MO); hills E of Tingo María, *Croat 21152* (MO). **Junín:** Prov. Satipo, Pichanaki, *León 226* (USM); Schunke Hacienda, above Ramón, *C. Schunke A214* (US); Chanchamayo Valley, *C. Schunke 165* (F, US), *666* (F), *1396* (F). **Loreto:** above Pongo de Manseriche, *Mexia 6246a* (UC, US); Aguaytia, *Croat 21014* (MO). **Madre de Dios:** Prov. Manu, town of Atalaya, 2–3 km W of village, *Foster 7455* (F, MO, USM); Pantiacolla, serranía across Río Alto Madre de Dios from Shintuya, *Gentry et al. 27365* (MO); prov. Manu, km 139 on road between Cabo de hornas and Shintuya, *Foster 4020* (F, USM); Parque Nacional de Manu, Cocha Cashu Biological Station, *Foster P-84-91* (F); valle de Marcapata, *Herrera 1200* (US). **Oxapampa:** Prov. Pasco, Iscoazin, *Foster 7937* (F, USM). **San Martín:** Mt. Campana, *Spruce 4337* (color slide of K specimen at MO; photo GH, US); Tarapoto, Ad rupes secus rivularum, Aug. 1855, *Spruce 4090* (photo of K specimen at GH; photo and fragment P, US); Prov. de Lamas, beween Tarapoto and Moyobamba, ca. 10 km NW of Tabalosas, *Croat 51154* (MO).

BOLIVIA. **La Paz:** Cordillera Real, Río Chimate, *Tate 502* (NY), *513* (NY); Mapiri, *Williams 1188* (NY, US); Mapiri, *Buchtien 1015* (US), *2138* (US); Mapiri region, San Carlos, *Buchtien 13* (US); Mapiri, Charopampa, *Buchtien 11* (MICH, P). **Prov. unknown:** Challana Riv., *Cardenas 1249* (LIL, US).

7. **Polybotrya crassirhizoma** Lellinger (Fig. 26, Map 4).

Polybotrya crassirhizoma Lellinger, Amer. Fern J. 62:49, figs. 1, 8. 1972. TYPE: Peru. Loreto: Gramitanacocha, Río Mazán, alt. 100–125 m, *J. Schunke 268* (holotype: US!; isotypes: F!, GH!, NY!, UC!).

Polybotrya macbridei Lellinger, Amer. Fern J. 62:51, figs. 2, 9. 1972. TYPE: Peru. Junín: Hacienda Schunke, La Merced, *Macbride 5602* (holotype: US!; isotype: F!).

Stem 1–2 cm thick, hemiepiphytic; *scales* 10–25 × 0.2–1.1 mm, dull orange or reddish brown, rarely shiny and dark brown, with a dark central stripe and lighter borders, rarely concolorous, margins denticulate to erose. *Sterile leaves* up to 1.35 m; *petiole* ½ to ¼ the length of the lamina, scaly at base; *lamina* lanceolate, to 1.0 × 0.44 m; *pinnae* 6–20 pairs, (11)15–20(24) × 2–4 cm, lanceolate to oblong-lanceolate, the base unequal, broadly rounded or truncate on the acroscopic side, slightly excavate or tapering on the basiscopic side, the margins crenate-dentate or more rarely lobate-serrate, apex acuminate, often serrate; *veins* free, often with a single veinlet springing from the costa between the main pinnate groups; *axes* with a few, scattered, narrow, appressed scales, occasionally pubescent, the hairs short, less than 0.1 mm, erect, colorless, subulate, unicellular. *Fertile leaves* 2-pinnate, occasionally 2-pinnate-pinnatifid in large individuals, ½ to ⅓ smaller than the sterile leaves; *axes* similar to those of the sterile leaves but with larger more numerous scales; *sori* coenosoric, completely covering the abaxial surface of the pinnules, occasionally discrete and round at the pinnule base; *sporangia* nonparaphysate; *spores* (48)52–56(61) microns long. $n = 41$.

Other illustrations: See original descriptions of *P. crassirhizoma* and *P. macbridei*, cited above.

Polybotrya crassirhizoma grows primarily in lowland forests of the western Amazon basin and in premontane forests of the eastern Andes (Map 4) from 100 to 1500 m. The cluster of dots in eastern Ecuador reflects recent collecting activity in that area and this species' true abundance there. I saw this species in nearly every forest that I visited in the Amazon basin of Ecuador, and it was one of the most frequent and abundant ferns. This abundance suggests that *P. crassirhizoma* occurs farther east in the Amazon basin than is shown in Map 4. Apparently, *P. crassirhizoma* flourishes on clayey soils and does not grow in sterile, sandy soils.

I chose the name *P. crassirhizoma* over *P. macbridei* because of the more widely distributed type collection. *Polybotrya crassirhizoma* and *P. macbridei* were said to differ by stem thickness, scale luster and color, and the presence versus the absence of lobing at the base of the sterile pinnae (Lellinger 1972). These characters, however, intergrade completely as shown by a series of specimens collected near Coca in the Amazon basin of Ecuador (*Moran 3616*). The most obvious character that supposedly distinguishes *P. macbridei* is the basally lobed pinnae, but this character represents the lobing that typically occurs in transitional sterile-fertile leaves. This example illustrates how part-fertile leaves can cause taxonomic confusion. Accordingly, I placed *P. macbridei* in synonymy.

Specimens examined: COLOMBIA. **Amazonas:** Loreto-Yaco, *Schultes & Black 46-266* (GH).

ECUADOR. **Napo:** 27 km SE of Coca, petroleum well Auca 4, *Moran 3616* (F, GH, NY, Q, QCA, US); 20 km NE of Coca, 5 km N of Joya de las Sachas, *Moran 3615* (F, GH, NY, PORT, Q, QCA, US); about 10 km SE of Tena, 3 km E of Puerto Nuevo on road to Puerto Mishahuallí, *Moran 3535* (F, GH, NY, Q, QCA, US); Bimbino, on the Río Pacuno, 10 hr W of confluence with Río Napo, *Whitmore 752* (BM); Río Cuyabeno, about 2 km upstream from Puerto Bolívar, *Brandbyge et al. 33684* (AAU); San Pablo de los Secoyas, *Brandbyge & Asanza C. 32881* (AAU); San Pablo de los Secoyas, Río Wai si aya, *Brandbyge et al. 32617* (AAU); San Pablo de los Secoyas, on path to Shushufindi, *Brandbyge et al. 32544* (AAU); 50 km NE of Coca, *Lugo S. 3293* (GH); Canton Putumayo, Río Aguarico, town of Dureno, *Plowman et al. 4025* (GH); Anagua, Parque Nacional Yasuni, SEF forest project area, *Øllgaard et al. 38836* (AAU), *39084* (AAU). **Pastaza:** Curaray, Valle de la Muerte, *Holm-Nielsen et al. 22484* (AAU, Q, QCA); basin of Río Pastaza, Pacayacu-Sarayacu region, *Gill 47* (NY); village of Río Chico, 8 km from Puyo, *Shemluck 280* (F); Río Bobonaza, between oil exploration camp Chichirota and Destacamento Cabo Pozo, *Øllgaard et al. 34855* (AAU, Q, QCA); Río Bobonaza, between Cachitama and the outlet of Río Bufeo, *Øllgaard et al. 34748* (AAU); Río Pastaza, near the Peruvian border, around Destacamento Ishpingo,

FIGURE 26. *Polybotrya crassirhizoma* Lellinger. a. fertile leaf; b. sterile leaf; c. fertile pinna; d. sterile pinna; e. stem scales. a: *Øllgaard et al. 34855* (AAU). b–e: *Moran 3615* (F).

Øllgaard et al. 34970 (AAU); 2 km W of Yuralpa, S border of Río Napo, *Holm-Nielsen & Jeppsen 987* (AAU).

PERU. **Huánuco:** Prov. Pachitae, Río Pozouso, *Foster 9284* (F, MO, USM). **Junín:** Chanchamayo Valley, *C. Schunke 157* (F), *158* (F), *661* (F), *812* (F); Schunke Hacienda, above San Ramón, *Killip & Smith 24605* (NY, US); E of Quimiri Bridge, near La Merced, *Killip & Smith 23876* (NY, US); Hacienda Schunke, La Merced, *Macbride 5602* (F, US); La Merced, Chanchamayo, *Soukup 1065* (F). **Loreto:** Prov. Maynas, Quebrada Yanomono, Explorama tourist camp, Río Amazonas above mouth of Río Napo, Transect 6, *Gentry et al. 27880* (MO), *Moran 3640, 3641* (F, Q, QCA); Mishuyacu, near Iquitos, *Klug 1386* (NY, US); Gamitanacocha, Río Mazán, *J. Schunke 268* (F, GH, NY, UC, US), *14285* (US); Veradera de Mazán, *Croat 20763* (MO); Río Napo near Entrada de Isla Inayuga, *Croat 20551* (MO).

BOLIVIA. **Cochabamba:** Prov. Carrasco, confluence of Río Leche with Río Isarsama, *Beck 1635* (LPB).

BRAZIL. **Acre:** Cruzeiro do Sul, vicinity of Serra da Moa, *Prance et al. 12180* (NY).

8. Polybotrya espiritosantensis Brade (Fig. 27, Map 21).

Polybotrya espiritosantensis Brade, Rodriguesia 10:28, tab. 3. 1948. TYPE: Brazil. Espírito Santo: Municipality of Itaguaçu, Jatiboca, virgin forest, 700–800 m, *A. C. Brade 18224* (holotype: RB!).

Stem 1–2 cm wide, hemiepiphytic; *scales* mostly 10–15 × 1.0–2.5 cm, bright reddish brown, spreading, membranous, the center often darkened to varying degrees, margins highly erose-denticulate, occasionally fimbriate. *Sterile leaves* up to 1.2 m long; *petiole* to 30 cm long, about half as long as the lamina, scaly at base; *lamina* ovate, 2-pinnate proximally, becoming 1-pinnate distally, 60–90 × 50–70 cm, subcoriaceous, pale green, nearly glabrous on both surfaces, the apex subconform and pinnalike but with one or two basal lobes; *pinnae* alternate, 6–8 pairs, the apex conform, like the lateral pinnules, the upper pinnae simple and resembling the pinnules of the lower; *pinnules* anadromic throughout, 3–4 pairs, elliptic, 10–13 × 2–3 cm, the margins entire, the apex acuminate, the base cuneate, the proximal pinnules with stalks 2–4 mm long, the distal pinnules sessile; *veins* slender, none conspicuously thicker than the others, long, parallel, 1–2 branched, the tips free; *axes* with a few scattered, appressed, narrow scales, otherwise glabrous. *Fertile leaves* 2-pinnate, amphiacrostichoid; *pinnules* caudate, entire, appearing cylindrical when mature; *sporangial stalks* paraphysate; *spores* (52)54–60(62) microns long.

Other illustrations: Brade's original description has an excellent photograph of the type; Brade, Bradea 1:67, tab. 6, fig. 5. 1971 (stem scales only).

Polybotrya espiritosantensis is endemic to the state of Espírito Santo in southeastern Brazil (Map 21). I expect this species will eventually be found in other parts of mountainous coastal Brazil. *Polybotrya espiritosantensis* has the most distinctive laminar cutting of any species in the genus. No other species has the simple, entire pinnules that evenly taper at the base and apex (Fig. 27b). Unlike all other species of *Polybotrya* that have pinnatifid apices, the leaf and pinnae apices of this species are conform or nearly so (Fig. 27a). The numerous, close, long, parallel veins (Fig. 27b) are like those of the 1-pinnate species *P. fractiserialis* and *P. sorbifolia* and probably indicate a close relationship.

Specimens examined: BRAZIL. **Espírito Santo:** Santa Thereza, 900 m, *Foster & Foster 854* (GH, US); Municipality of Itaguaçu, Jatiboca, virgin forest, 700–800 m, *A. C. Brade 18224* (RB).

POLYBOTRYA subgenus POLYBOTRYA

TYPE SPECIES: *P. osmundacea* Willd., Sp. Pl. ed. 4, 5:99. 1810.

Polybotrya subgenus *Eupolybotrya* Fée, Mém. Fam. Foug. (Hist. Acrost.) 2:16. 1845.

Acrostichum section *Polybotrya* Hooker, Species Filicum 5:244. 1864.

Stem hemiepiphytic; *sterile leaves* 1-pinnate-pinnatifid to 4-pinnate; *veins* free.

9. Polybotrya caudata Kunze (Fig. 28, Map 5).

Polybotrya caudata Kunze, Linnaea 9:23. 1834. TYPE: Peru. Huánuco: Pampayaco, July 1829, *Poeppig s.n.* (B!).

Polypodium adiantoides Aublet, Hist. Pl. Guiane Françoise 2:962. 1775, *nomen illeg.*, *non* Burm. (1768). TYPE: Guyana. *Aublet s.n.* (holotype: BM!, Morton photo 6626 at B!, F!, GH!).

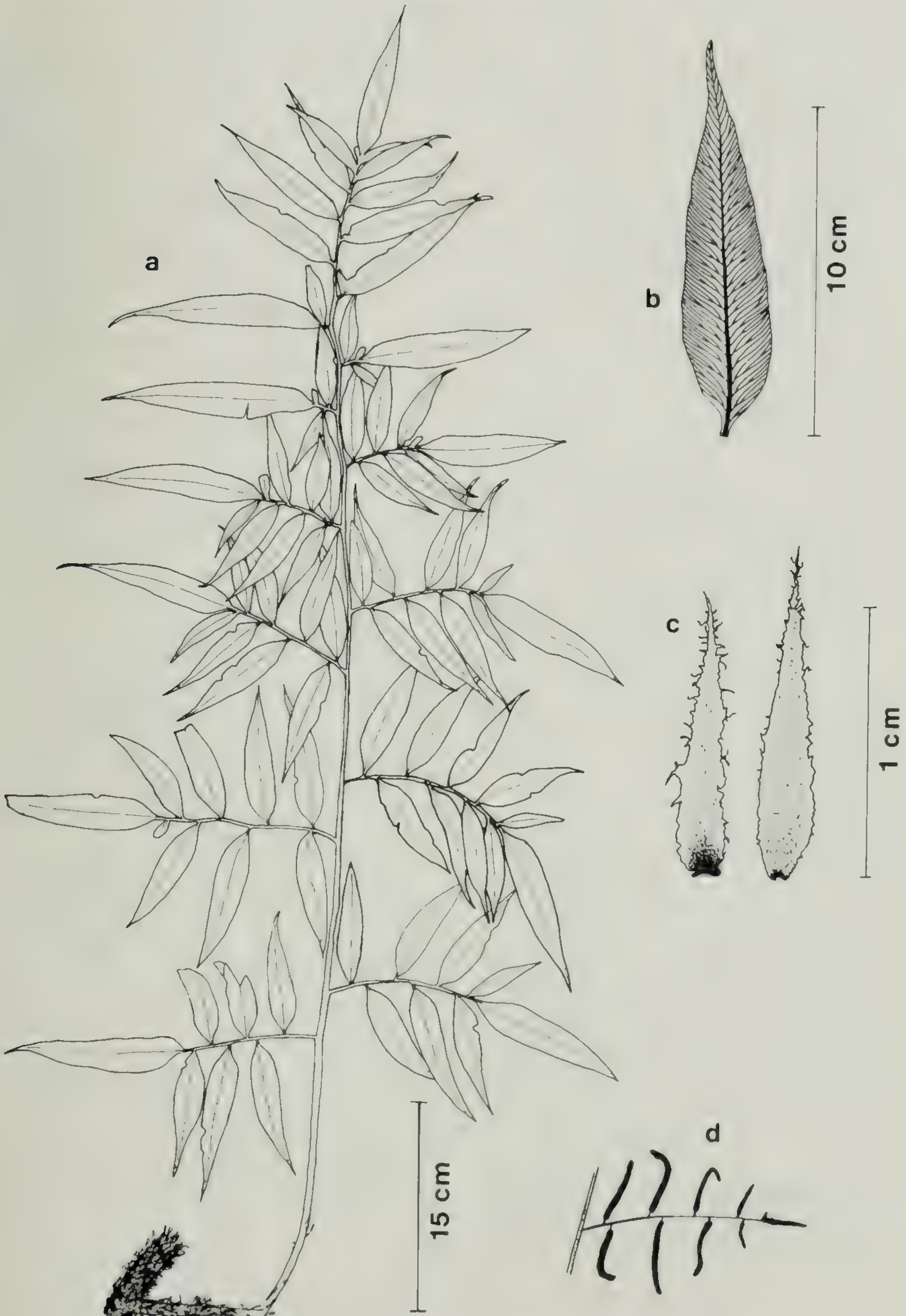

FIGURE 27. *Polybotrya espiritosantensis* Brade. a. sterile leaf; b. sterile pinnule; c. stem scales; d. fertile pinna. a–d: *Brade 18224* (RB).

Olfersia caudata (Kunze) Kunze, Linnaea 21:206. 1848.

Psomiocarpa caudata (Kunze) Presl, Epim. Bot. 162. 1849.

Acrostichum caudatum (Kunze) Hooker, Species Filicum 5:244. 1864. *nomen illeg. non* Hooker (1840).

Polybotrya acuminata Kaulfuss var. *villosa* Christ, Prim. Fl. Costar. 3(1):9. 1901. TYPE: Costa Rica. Limón: Llanuras de Santa Clara, 500 m, *Biolley 10688* (lectotype: US!; isotype: CR!).

Polybotrya villosula Christ, Bull. Herb. Boissier, II. 6:168. 1906. TYPE: Costa Rica. Santa Clara, Las Delicias, 1897, 500 m, *Pittier 10688* (P?).

Polybotrya costaricensis Brade, Bradea 1:11, tab. 1, fig. 1. 1969. TYPE: Costa Rica. Limón: Hundrisser Ranch, Atlantic shore, Sept. 1909, *Brade & Brade 374* (holotype: HB; isotypes: NY!, UC!).

Stem 0.5–2.5 cm thick, hemiepiphytic; *scales* linear-lanceolate to narrowly triangular, 8–20 × 1–2 mm, dull brown, opaque, entire to denticulate, the base elevated, thickened, curved, and appressed. *Sterile leaves* up to 2 × 1 m; *petioles* 30–70 cm long, about ⅓ the length of the lamina; *lamina* mostly 2-pinnate-pinnatifid, rarely 3-pinnate at the base, firm-chartaceous, glabrous to pilose, the hairs 0.2–1.5 mm long, acicular, the margins sparsely ciliate, the hairs minute, less than 0.2 mm long; *pinnae* up to 20–45(60) × 7–20(30) cm, subdeltate, acuminate, subequilateral, slightly more developed on the acroscopic side; *pinnules* slightly prolonged acroscopically, the base truncate to slightly cordate, catadromically arranged in the medial pinnae; *veins* free, sometimes with a single vein springing from the costa between the pinnate groups; *axes* nearly glabrous or pubescent to various degrees, the hairs acicular, whitish; *grooves* usually pubescent within, often densely so at the junctures. *Fertile leaves* similar in size to the sterile, mostly 2-pinnate, but with some of the larger pinnules lobed at base; *pinnae* caudate, 4–8(11) × 0.5–1.5 cm, apparently soriferous on both surfaces; *spores* (43)46–50(53) microns long. $n = 41$.

Other illustrations: Fée, Mém. Fam. Foug. (Hist. Acrost.), Atlas, tab. 34, 1845; Vareschi, Fl. Venez., vol. 1, tab. 73. 1968; Brade, Bradea 1(9):63, fig. 1; p. 67, fig. 6.; Croat, Fl. Barro Colorado Is., figs. 28 & 29. 1978 (as *P. villosula*); Stolze, Fieldiana Bot. n.s. 6, fig. 60a,b. 1981; Tryon & Tryon, Ferns & Allied Plants, figs. 80.8, 80.9, 80.22, 80.23. 1982.

Polybotrya caudata is one of the most widely distributed species in the genus (Map 5). It grows primarily in lowland forests from sea level to 800 m, but specimens from the Andes have occasionally been collected as high as 1900 m. I found this species at many of the sites where I collected in Costa Rica, Ecuador, and Peru, but not in Venezuela. *Polybotrya caudata* is one of only three species in the genus that occur on an oceanic island—Cocos Island, about 500 km (310 mi) southwest of Costa Rica.

Polybotrya villosula was said to differ from *P. caudata* only by its long and villous pubescence, but specimens are usually glabrous or fully pubescent, with few intermediate forms. Since pubescence does not correlate with any other character and I found no difference in geographical range between the two forms, I regard *P. villosula* as a synonym of *P. caudata*.

The juvenile leaves in glabrous plants of this species may be difficult to distinguish from *P. osmundacea*. A good character to separate the two species is the minutely and sparsely ciliate leaf margin of *P. caudata* (Fig. 28a); that of *P. osmundacea* is always glabrous (Fig. 47). The thick, dull brown, curved, and appressed stem scales (Fig. 28b,h) also help distinguish *P. caudata* from many other *Polybotrya* species.

Specimens examined: MEXICO. **Chiapas:** eastern highlands near Guatemalan border, *Breedlove 34101* (CAS).

GUATEMALA. **Alta Verapaz:** near Río Icvolay, near Hacienda Yaxcbnal, 5 mi NW of Cubilquitz, 250–300 m, *Steyermark 44675* (F); Cubilquitz, 350 m, *Tuerckheim 148* (US), *358* (P, Z), *7812* (US), 8040B (US), *8041* (GH, NY). **Izabal:** between Bananera and "La Presa" in Montaña del Mico, *Steyermark 38229* (F), *38271* (F), *39197* (F); Río Chacón, 30 m, *Johnson 1221* (US); between Los Amates and Izabal, Sierra del Mico, *Kellerman 7354* (F, NY); along Río Frío, 65 m, *Steyermark 39895* (F, US); 2.5 mi N of Río Dulce on gravel road to Petén, *Dunn & LeDoux 22005* (MO, NY); vicinity EXMIBAL Camp 2 (La Gloria), NW of Lake Izabal, 400–500 m, *Jones & Facey 3246* (NY); vicinity of Quirigua, *Standley 24195* (GH); vicinity of Puerto Barrios, *Standley 25085* (GH, US).

BELIZE. **El Cayo:** Vallentin, *Lundell 6416* (GH, US). **Stann Creek:** along road and stream at Dry Creek, near Dist. of Cayo Border, *Croat 24541* (CR, MO); Middlesex, *Gentle 2947* (GH, MICH, US); *Schipp 273* (BM, F, GH, MO, UC, US, Z).

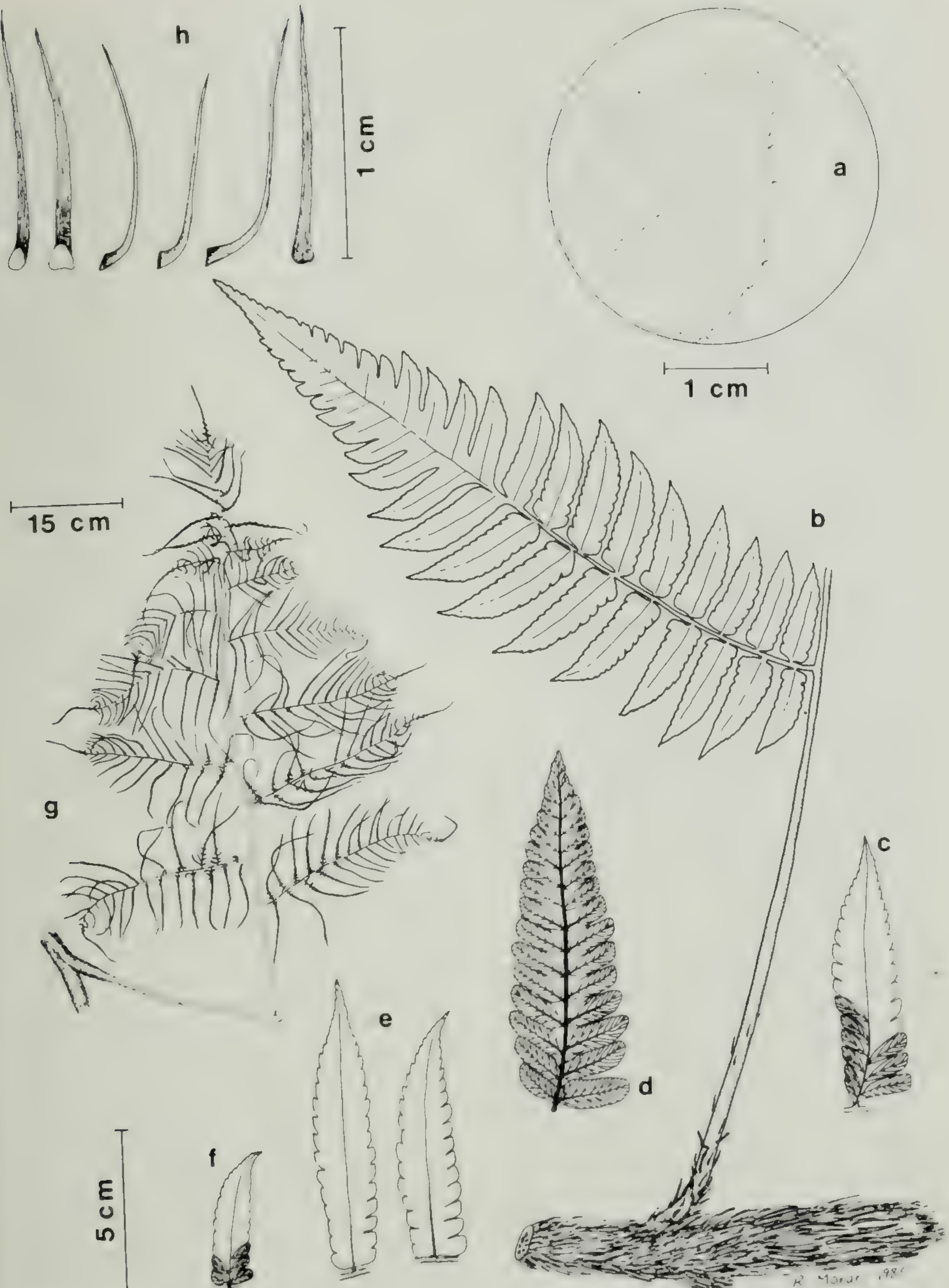

FIGURE 28. *Polybotrya caudata* Kunze. a. leaf margin showing minute cilia; b. stem and basal pinna (note appressed scales—same scale as f); c–f. acroscopic pinnules, pinnae apex toward the right in all; g. fertile leaf; h. stem scales, abaxial view at left, side view in center, adaxial view at right. a,c: Costa Rica, *Scamman 7156* (GH). b: French Guiana, *Cremers 7369* (CAY). d,g,h: Costa Rica, *Moran 2186* (F). e: Bolivia, *Steinbach 7499* (MO). f: Trinidad, *Fendler 105* (GH).

HONDURAS. **Atlántida:** Lancetilla Valley, near Tela, *Standley 53983* (F, US); near Ceiba, 400 m, *Dyer A225* (US).

NICARAGUA. **Chontales:** 4 km al oeste de La Libertad, El Comatillo, *Gómez & Cittar 6731* (CR); vicinity of La Libertad, 500–700 m, *Standley 9047* (F). **Zelaya:** road to Mina Nueva Americana, *Stevens & Krukoff 12666* (CR, MO); along new road from Río Blanco to Río Copalar, *Stevens & Krukoff 12056* (CR, MO); Caño Aamora on Río Rama, *Stevens & Krukoff 8827* (CR, MO); base camp 3.6 km SE Cerro San Isidro, Río Kama, Río Escondido, 0–65 m, *Proctor et al. 27091* (F, NY, VEN); Mosquito Coast, *Schramm s.n.* (US); Bluefields, *Niell 2610* (CR); area de la Bahía de Bluefields, Río Escondido, 0–30 m, *Molina R. 1907* (F, US); near Bluefields, *Danneberger s.n.* (US); Braggman's Bluff, *Englesing 291* (F, US); Mina Nueva Americana, 11.3 km N of main road, *Pipoly 5299* (CR, MO); 13 mi above Kururia, *Pipoly 3824*; Colonia Kururia, *Pipoly 3880* (CR, MO), *3901* (CR, MO); Neptune Mining Co., *Stevens & Krukoff 13005* (CR, MO); near junct. of road to Alimidkanba with road between El Empalme and Limbiaka, *Stevens & Krukoff 12741* (CR, MO); Apz. 5 km de Rama sobre el Río Rama, *Gómez & Cittar 6409* (CR); El Salto along Río Pis Pis, *Pipoly 3542* (CR, MO); 13 mi above Kururia on road to San Jerónimo, *Pipoly 3817* (CR, MO).

COSTA RICA. **Cartago:** near Turrialba, slope of the Río Reventazón behind the Instituto Interamericano de Ciencias Agricolas, 600 m, *Mickel 3368* (NY); Valley of Río Reventazón 9 km ENE of Turrialba near Pavones, 650 m, *Holm & Iltis 200* (F, NY). **Cocos Island:** *Barclay 2199* (BM); Wafer Bay, *Gómez 3354* (CR, F, US, Z); *Gòmez 4528* (CR); Chatham Bay, *Jiménez M. 3200* (CR, GH). **Heredia:** Holdridge's Finca La Selva, Río Puerto Viejo at Quebrada El Sura and Q. El Salto, *Rossbach 3710* (GH), *Scamman 7482* (GH), *Scamman & Holdridge 7998* (CR, GH); 2 km upstream from confluence of Río Puerto Viejo with Río Sarapiquí, Finca "La Selva," *Burger & Stolze 5865* (CR, F, GH, US), *Mickel 3570* (NY). **Limón:** Llanuras de Santa Clara, *Biolley 10688* (CR, US); Hundrisser Ranch, Atlantic slope, *Brade & Brade 374* (NY, UC); 7 km SW of Bribri, 100–250 m, *Gómez et al. 20423* (CR, MO, UC); N end of Tortuguero Natl. Park, *Burger & Antonio 11263* (CR, F, NY); near Guápiles, at bridge over Río Guácimo, 50 m, *Moran 2182, 2185, 2186* (CR, F, P, PORT); near banana plantation and Pandora, near Río Estrella, *Rossbach 3624, 3625* (GH); La Lola, a cacao finca, near Río Madre de Dios, *Scamman 7156* (GH); Finca Montecristo, on the Río Reventazón below Cairo, 25 m, *Standley & Valerio 48622* (US). **Puntarenas:** Osa Peninsula, *Mickel 1944* (CR, NY); hills N of Palmar Norte, along trail to Jalisco, *Croat 35176* (MO); Osa, 40 km W of IA rt. 2, *Gómez 19489* (CR, MO).

PANAMA. **Bocas del Toro:** in Laguna de Chiriquí and its neighborhood, *Hart 53* (US). **Canal Zone:** "Isthmo Panama," *Hayes 8* (B, GH, Y, US); hills N of Frijoles, *Standley 27597* (MO, US); Cerro Azul, *Tyson 2109* (MO); along hogback ridge S of Fuertes Cove, Pearson Peninsula, *Croat 8153* (MO); headwaters of the Río Chinilla, above Nuevo Limón, *Maxon 6895* (US); ravine near Frijoles, *Killip 2929* (US); along riverbank between Fort Sherman and Fort Lorenzo, *Croat & Porter 15436* (MO); hilly forest around the Agua Clara Reservoir, near Gatun, 20–30 m, *Maxon 4641* (GH, NY, US); Orange River Trail, *Cornman 544* (UC, US); Barro Colorado Island, Gatun Lake, *Maxon et al. 6817* (GH), *Seaverns 56* (F), *Starry 91* (F, GH), *Croat 5114* (MO), *6850* (MO), *7362* (MO), *8025* (MO), *9000* (MO, NY), *9004* (MO, UC), *9103* (COL, MO, UC), *10804* (MO), *15256* (MO), *17367* (F, MO), *Bailey & Bailey 541* (GH), *Chrysler 4836* (UC); 10 mi from main gate, near Río Frijolito, *Croat 15081* (F, MO, US); Allison Armour Trail, *Wetmore & Woodworth 130* (GH). **Chiriquí:** above Río San Felix near town of San Felix, ca. 13 mi N of Río San Felix bridge, 800–1200 m, *Croat 33452* (MO); forest behind Vivero forestal, 12 km N of Los Planes de Hornito, IRHE Fortuna Hydroelectric Project, 1200–1300 m, *Knapp 4966* (MO). **Colón:** Santa Rita Ridge, end of road from Transisthmian Highway, ca. 10 mi from road, *Porter et al. 4763* (MO); Santa Rita Ridge, 2.8 mi from Boyd–Roosevelt Hwy., *Croat & Porter 15342* (F, MO); forest along Portobelo–Nombre de Dios road, 10 km W of Nombre de Dios, *Knapp & Mallet 5402* (MO). **Darién:** vicinity of Cana, summit of knoll above Cana, *Stern et al. 523* (GH). **Panamá:** 2.5 mi N of Goofy Lake on road to Cerro Azul, *Croat 11544* (F, MO); upper Mamoni River, 150–400 m, *Pittier 4492* (US); Orange River Valley, E of Juan Diaz, *Killip 2544* (GH, US); along Río Pirati, foothills of the Serranía de Maji, *Knapp & Mallet 5133* (MO); in high ridges of the Serranía de Maji, S of the Chocó village of Ipeti, *Knapp et al. 4479* (MO); along Juan Diaz River, 4 mi above Juan Diaz, 0–75 m, *Killip 2845* (US). **San José Island:** Perlas archipelago, Gulf of Panama, 55 mi SSE of Balboa, *Johnston 452* (GH, US). **Veraguas:** Isla de Coiba, *Mendez 75* (MO).

TRINIDAD. Aripo road via Arima, *Broadway 5717* (F, Z); without locality, *Fendler 105* (GH, MICH, MO, NY, P, PH, UC); without locality, *Broadway 5358* (NY); forest, Brazil, *Britton et al. 2144* (GH, NY); Mount Tamana, *Britton et al. 1935* (NY); Oropuche, local road via Valencia, *Broadway 9207* (MO, UC); without locality, *Crueger 139* (B); La Sierra, Maraval, *Hombersley s.n.* (MO); Arima Ward, Guanapo River Valley, ca. 1 mi SE of La Leja village, *Jermy 3122* (BM); Cumaca Road, *Fay 472* (BM); Brickfield's Tea Plantation, 3 mi S of Forestry Rest House, *Jermy 2137* (BM); Valencia Ward, near Valencia, *Jermy 10826* (BM); Hollis Reservoir Road, *Mickel 9472* (UC).

FRENCH GUIANA. Saint Jean du Mearoni, *Benoist 1271* (P); Central Guyana, *Leprieur s.n.* (P); Sommet Tabulaire, 650–750 m, ca. 45 km SE of Saul, *Cremers 6374* (CAY), *6523* (CAY, Z); Bassin du Haut Inipi, 7 km WSW du Pic Coudreau (Monts Bakra), *Granville 4012* (CAY, Z); Haut Oyaopock, W of Trois Sauts Crique Euleupousing, rive gauche du Saut Cambrouse,

Granville 1143, 1165 (CAY, NY, Z); S of Tampoc: Saut Koumakou Soula, *Cremers 4460* (CAY, Z); Saut Tampoc, *Granville 4841* (CAY); Haute Riv. Mana: Saut Grous Tigre, *Cremers 7552* (CAY, Z); Haute Crique Baboune, affluent de la Riv. Mana, *Cremers 7369* (CAY, Z); Haute Crique Waamahpann, au depart du chemin indien, *Granville 971* (CAY); Frontiere Guyane–Surinam, Tuma Humac, *Granville 991* (CAY, Z); Crique Gabaret, 25 km de l'embouchure, layon N–W, *Oldeman 1933* (CAY, NY); Crique "Roche Fende" (affleunt de la Comte) a 1 km environ de son embouchure, *Granville B.4711* (CAY, Z); W of Saul on trail to Monts Galbao, *Boom & Mori 1856* (CAY, NY); Piste allant de Citron vers le Massíf du Decou Decou, *Billiet & Jadin 1683* (CAY); Región de Paul Massíf du Decou Decou, *Cremers 7951* (CAY, Z).

SURINAM. West Rivier, 2–5 km SW of Juliana Top, 275–300 m, *Irwin et al. 54896* (NY); no locality, *Hostmann s.n.* (NY); 45 km S of Paramaribo, new road to Hanover, N of Zanderij, *Tryon & Kramer 5611* (GH, MICH, NY); about 25 km S of Paramaribo, *Lindeman 4570* (GH), *Kramer 1954* (MO); 3 km S of Juliana Top, 12 km N of Lucie River, 300–325 m, *Irwin 55161* (MO, NY); Para Dist., *Lindeman & Teunissen 15291* (Z); Suriname River, Plantage "Accaribo," *d'Angremond s.n.* (Z).

GUYANA. Kamuni Ck., Groete Ck., Essequibo River, *Maguire & Fanshawe 22855* (GH, NY); Essequibo River, *Persaud 372* (F); Rockstone, *Gleason 582* (GH, NY); Demerara, *Jenman s.n.* (NY); Barima River, *Jenman s.n.* (NY); 3 mi S of Chodikas, *Guppy 462* (BM); Essequibo River, Moraballi Ck., near Bartica, *Richards 803* (BM); lower Cuyuni River, *Sandwith 1561* (BM).

VENEZUELA. **Bolívar:** Dtto. Heres, Campamento Guri, *Fernández 951* (PORT, UC); Roraima, *Schomburgk s.n.* (B, NY); without locality, anno 1843, *Schomburgk 1659* (B); E of Cerro El Picacho, N of Las Nieves and Las Chicharras, 45 km N of Tumeremo, vicinity of Beborah, Altiplanicie de Nuria, 600–650 m, *Steyermark 89120* (NY, VEN); a lo largo de la Quebrada Acarabisí, limites del Estado Bolívar con la zona dereclamación, *Aymard et al. 952* (PORT, UC). **Portuguesa:** Depto. Paez, Pozo Blanco, entre Acarigua y Payara, 190 m, *Ortega 636* (PORT, UC, VEN). **Sucre:** selva del Rectangulo N del Lago de Tuanoco, *Lasser & Vareschi 3926* (VEN); vicinity of Cristóbal Colón, Avicagua, *Broadway 560* (GH, NY, US). **Territorio Federal Delta Amacuro:** Depto. Antonio Diaz, 9°15′N, 60°57′W, upper reaches of riverine forest of Caño Atoiba tributary of Boca Araguao, *Steyermark et al. 115033* (VEN); Depto. Antonio Diaz, vicinity of Caño Jotajana (= tierra alta), tributary of Caño Guiniquina, NW of Epana near boundary with Depto. Tucupita, 9°15′N, 61°10′W, 50 m, *Steyermark et al. 115021* (MO, UC, VEN); Depto. Pedernales (boundary with Depto. Tucupita): Caño Simoina, west of Isla Coucuina, S of Barra de Coucuina, 50 m, *Steyermark et al. 114331* (MO, VEN), *114332* (MO, UC, VEN).

COLOMBIA. **Amazonas:** Trapecio Amazonico, Loretoyacu River, 100 m, *Schultes & Black 8467* (GH, US). **Cauca:** Cali, *Lehmann 2998* (BM); en la orilla opuesta Puerto Limón–Río Caqueta, *Mora 4430* (COL); Gorgona Island, off Nariño, *Taylor 1223* (MICH, NY); Río Timbiqui, *B.T. 443* (GH). **Chocó:** slopes and ridge of Loma del Cuchillo, ca. 15 km WSW of Chigorodó, 150–400 m, *Lellinger & de la Sota 643* (LLP, US); upper Río Truando, 2 km SSW of the confluence of Río Nercua near the MADUREX Camp, 100 m, *Lellinger & de la Sota 589* (COL, LP, US); trail to Miniquia E of Puerto Mutis (Bahía Solano), 20–120 m, *Lellinger & de la Sota 26* (CR, COL, LP, US); Río San Juan, 3.5 km SW of Andagoya, just NE of the mouth of the Río Suruco, 60 m, *Lellinger & de la Sota 496* (COL, LP); Municipio de Río Sucio, Parque Nacional Los Catios, alrededor del Campamento de Tilupo, 250–320 m, *Forero & Jaramillo 1745* (COL, MO). **Cundinamarca:** Cordillera Oriental, Mesa Negra, Gazuguan Valley, 6 km NW of Medina, 580 m, *Grant 10436* (F, US). **El Valle:** La Cumbre, Cordillera Occidental, 1700–2200 m, *Killip 11343* (GH, NY, US); Finca La Pradera ca. 6 km SW of El Cairo on trail to Río Blanco, between El Brillante and Boquerón, *Lellinger & de la Sota 790* (COL, US). **Nariño:** Pambana, between Río Pimbi and Río Cuembi, on Río Telembi, above Barbacoas, 50 m, *Ewan 16846* (BM, GH, UC).

ECUADOR. **Los Ríos:** Río Palenque biological station, km 56 Quevedo–Sto. Domingo road, *Evoy 104* (NY). **Morona-Santiago:** Pachicutza, at "Escuela iscomisional [*sic.*] Cardinal Dofner," km 140 on road Loja Gualaquiza, 900–1000 m, *Holm-Nielsen et al. 4489* (AAU, Q, QCA), *4495* (AAU, Q, QCA); Sucua, *Swingle et al. 70-02-05-2* (UC, US). **Napo:** casi 10 km SE de Tena, 3 km este de Puerto Nuevo por camino a Puerto Misahuallí, 300 m, *Moran 3534* (F, Q, QCA); 10 km al sur de Tena a Puerto Misahuallí, *Moran 3588* (Q, QCA); Anangu, Parque Nacional Yasuni, SEF project, 260–350 m, *Øllgaard et al. 38932* (AAU, Q, QCA); 27 km SE of Coca, *Moran 3617* (MO, C, QCA). **Pastaza:** Río Bufeo, northern tributary of Río Bobonaza, 300 m, *Øllgaard et al. 43798* (AAU, Q, QCA); Río Bobonaza, around houses between Huagracachi and Cachitama, below Montalvo, 300 m, *Øllgaard et al. 34634* (AAU, Q, QCA); oil exploration camp Chichirota, on the Río Bobonaza, 300 m, *Øllgaard et al. 35290* (AAU, Q, QCA). **Sur de Santander**: vicinity of Barran ca Bermeja, *Haught 1325* (MO).

PERU. **Amazonas:** Prov. de Bagua, left bank of Río Marañon opposite Quebrada Mirana (opposite km 277 of Marañon road above Cascadas de Mayasi), 425–450 m, *Wurdack 2011* (GH, US, USM). **Cuzco:** Prov. La Convención, 73°40′W, 12°30′S, at Camp Zero, 710 m, *Dudley 11513* (GH, US); Camp 1, 910–940 m, in J. Knox's quadrate, *Dudley 10168* (GH); Prov. Paucartambo, Mautainiza [?], 800–900 m, *Vargas 17800* (GH). **Huánuco:** Tingo María, 615–1100 m, *Allard 22593* (US); Cuchero, *Poeppig s.n.* (BM); hills

E of Tingo María, *Croat 21191* (MO); 10 km S of Tingo María, *Stork & Horton 9509* (F, UC, US); Pampayaco, *Poeppig 201* (B). **Loreto:** Prov. Maynas, Peter Jensen's Explorama Lodge, 50 mi downriver from Iquitos at Yanamono Ck., *Moran 3663* (AMAZ, USM); Prov. Maynas, about 10 km SW of Iquitos at zoological park, *Moran 3671* (AMAZ, USM); Pebas on the Amazon River, *Williams 1739* (F); Caballo-Cocha on the Amazon River, *Williams 2137* (F); Río Mazan, 100–125 m, *C. Schunke 380* (GH, NY); Prov. Maynas, Río Itaya, 10 km S of Iquitos, *Tryon & Tryon 5204* (GH); lower Río Huallaga, 155–210 m, *Williams 3999* (F, US); Quebrada Nawampa, *Croat 17620* (MO); Puerto Arturo, lower Río Huallaga below Yurimaguas, 135 m, *Killip & Smith 30690* (NY, US); Mishuyacu, near Iquitos, 100 m, *Klug 1166* (F, NY, US); Quebrada Tahuayo above Tamishiyaco, *Croat 19717* (MO); Río Itaya above Iquitos, *Croat 19220* (MO); primary forest 17 km SW of Iquitos on road to Puerto Almendara, *Croat 18388* (MO); 12 km SW of Iquitos, *Croat 18219* (MO). **Madre de Dios:** 12°49′S, 69°17′W, Prov. Tambopata, Tambopata Nature Reserve, ca. 30 air or 70–80 river km SSW of Puerto Maldonado at effluence Río Torre/Río Tambopata, 260 m, *Barbour 4764, 4790* (F, MO); Parque Nacional de Manu, Cocha Casha Biological Station, *Foster P-84-42* (F). **Pasco:** Puerto Bermudez, 375 m, *Killip & Smith 26637* (NY, US). **Puno:** San Gaván, *Lechler 2321, 2329* (B). **San Martín:** San Roque, 1350–1500 m, *Williams 7681* (F, US); Cerro de Campana, *Spruce 4634* (P).

BOLIVIA. **La Paz:** Prov. Sud Yungas, Límite de los Deptos. La Paz/Beni, Río Quiquibey, 320 m, *Beck 8037* (LPB); San Carlos, Mapiri, Mapiri River, *Tate 422* (LPB, NY); Mapiri, *Buchtien 35* (B), *290* (NY, UC). **Santa Cruz:** Prov. Sara, Río Yapaicani, 400 m, *Steinbach 7499* (B, F, GH, MO, Z); bosque del Río Surutú, 400 m, *Steinbach 3032* (US).

BRAZIL. **Acre:** Cruziero do Sul vicinity, Rio Moa between Igarape Ipiranga and Aquidaba, *Prance et al. 12069* (F, LP, NY, UC). **Amazonas:** prope São Gabriel da Cachoeira, ad Rio Negro, *Spruce 2116* (B, BM, P, RB); Larges, on the Amazon River 1 km below mouth of Rio Negro, *Conant 940* (F, GH, NY). **Pará:** Serra dos Carajás, AMAZ camp AZUL, *Sperling 5914* (GH, NY); Belém, *Huber 2599* (BM), *7235* (BM).

10. Polybotrya goyazensis Brade (Fig. 29, Map 6).

Polybotrya goyazensis Brade, Bradea 1:24, tab. 1, fig. 1. 1969. TYPE: Brazil. Goiás: Goiania, primary forest, December 1936, *A. C. Brade 15373* (holotype: RB!; isotype: NY!).

Polybotrya macedoi Brade, Bradea 1:24. 1969. TYPE: Brazil. Goiás: Municipio Jataí, Localidad Balsans, 1 November 1950, *Macedo 2682* (holotype: HB; isotypes: HB, MO!, SP, US!; paratypes: Brazil. Goiás: Fazenda Queixado, 8 December 1948, *Macedo 1447* (RB, SP); Fazenda Balsamo, 15 December 1948, *Macedo 1521* (SP).

Stem 1–2.5 cm thick, hemiepiphytic; *scales* spreading, membranaceous, generally 6–12(16) mm long, dark castaneous or dark reddish with lighter borders, margins strongly denticulate to erose, the base cordate to various degrees, often black and sclerified at the point of attachment. *Sterile leaves* up to 1.45 m long; *petiole* ⅓ to ½ as long as the lamina; *lamina* mostly 2-pinnate-pinnatifid, lanceolate to ovate, 1.2×0.9 m, the abaxial surface nearly glabrous to densely pubescent, the hairs whitish, acicular, up to 1 mm long, glands occasionally present, these reddish, sessile, resinous; *pinnae* up to 45×23 cm, lanceolate to narrowly deltate, the suprabasal ones soon becoming pinnatifid; *pinnules* narrowly deltate, mostly falcate, catadromically arranged above the base, $4–8(10) \times 1–2(3)$ cm, the acroscopic side slightly prolonged, the margins entire to crenate, ciliate, the hairs minute, 4–10 celled; *axes* nearly glabrous abaxially or densely pubescent, by tiny, unicellular hairs, scales very small or lacking, adaxially pubescent in the central groove with reddish hairs, 0.3–0.8 mm long; *grooves* usually ciliate on the ridges. *Fertile leaves* 2-pinnate, amphiacrostichoid; *pinnules* caudate, often lobed or undulate at the base; *sporangial stalks* paraphysate; *spores* (44)48–62(70) microns long.

Other illustrations: See original description of *P. goyazensis*; Sehnem, Fl. Ilust. Catarinense, pl. 18, 1979.

Polybotrya goyazensis occurs in Paraguay—the only species of *Polybotrya* known from that country—and in the southern half of Brazil but not in the coastal mountains (Map 6). This range is unusual because it comprises regions apparently not occupied by other species of *Polybotrya*. I suspect that *P. goyazensis* evolved from southernmost, isolated populations of *P. caudata*.

Polybotrya goyazensis has stem scales that are spreading, shiny, membranaceous, translucent, darkened in the center with lighter borders, margins strongly denticulate to erose, and the base cordate around the darkened point of attachment (Fig. 29f). In contrast, *P. caudata* has stem scales that are curved, appressed, thick, dull brown, concolorous, margins entire, and attached across the length of the thickened base (Fig. 28h). The minute cilia on the margins of the lamina serve to distinguish these two species from almost all other species of *Polybotrya* (Fig. 28a).

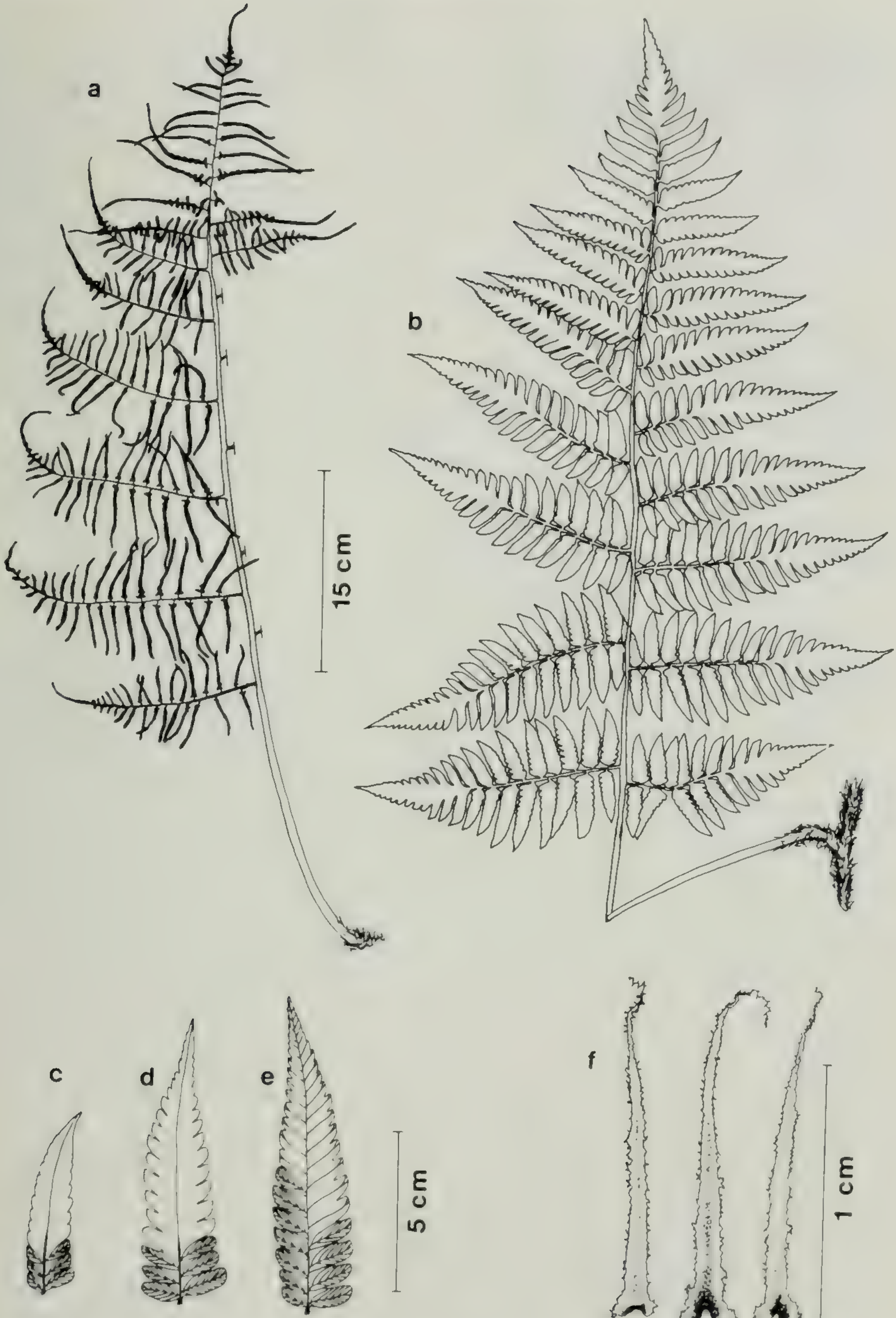

FIGURE 29. *Polybotrya goyazensis* Brade. a. fertile leaf; b. sterile leaf; c–e. proximal acroscopic pinnules; f. stem scales. a,b: *Rojas 10431* (B). c: *Brade 15373* (RB). d: *Prance & Selva 59677* (NY). e,f: *Argent et al. 6336* (UC).

Brade (1969c) distinguished *P. macedoi* from *P. goyazensis* by the former's pilose hairs on the axes and its slightly darker scales with lighter borders and a longer acuminate tip. These differences are not constant. Various degrees of pubescence exist, from densely pilose to nearly glabrous. This intergradation is shown by the type of *P. goyazensis:* the holotype at RB is nearly glabrous but the isotype at NY is densely hirsute. Examination of the stem scales shows a complete gradation of color, sometimes even on a single specimen.

Specimens examined: BRAZIL. **Goiás:** Goiania, primary forest, December 1936, *A. C. Brade 15373* (RB, NY); Serra do Caiapo, 40 km S of Caiaponia, *Prance & Silva 59677* (NY); Municipio Jataí, Localidad Balsans, *Macedo 2682* (MO, US). **Federal District:** "Brasilia," *Glaziou 14456* (B, P). **Mato Grosso:** 270 km N of Xavantina, 12°54′S, 51°52′W, *Ratter et al. 2047* (MO); Municipio Brilhante, Rio Anhanduí, *Hatschbach 25118* (UC); Expedition Base Camp, Brejo, 12°49′S, 51°46′W, *Argent & Richards 6651* (NY); 49.5 km N along road from base camp, *Harley et al. 10922* (NY); Xavantina, ca. 4 km N of ferry, *Argent et al. 6336* (RB, UC). **Pará:** no locality, 1914, *Petelot s.n.* (F).

PARAGUAY. Southern Paraguay, Sierra de Amambay, *Rojas 10182* (B, BM), *10431* (B, L, LIL, M, MICH, P), *10804* (B, BM, L); no locality, *Hassler 11618* (MICH).

11. Polybotrya pubens Martius (Fig. 30, Map 6).

Polybotrya pubens Martius, Icon. Plant. Crypt. Brasil. 87, tab. 25. 1834. TYPE: Brazil. ad flum. Amazonas prope Serpa, September, *Martius s.n.* (holotype: M).

Polybotrya pubens Kunze, Linnaea 9:22. 1834. *non* Martius. TYPE: Peru. Loreto: Prov. Maynas, ad Yurimaguas, September 1830, *Poeppig s.n.* (lectotype: P!).

Acrostichum pubens (Kunze) Hooker & Baker, Synopsis Filicum 414. 1868.

Acrostichum caudatum (Martius) Hooker var. *pubens* (Martius) Baker, Fl. Brasil. 1(2):586, tab. 38, figs. 1,2. 1870.

Dryopteris guentheri Rosenstock, Feddes Repert. 25:59. 1928. TYPE: Bolivia. La Paz: region of Mapiri, San Carlos, 15 November 1926, *Buchtien 260* (holotype: UC!).

Polybotrya crespiana Bosco, Nouvo Giorn. Bot. Ital., II. 45:145, tab. 9, fig. 1. 1938. TYPE: Ecuador. Santiago–Zamora: Indanza, *Crespi s.n.* (type not found, known only from Bosco's fig. 1).

Polybotrya decorata Lellinger, Amer. Fern J. 62:54, figs. 5, 6, 11. 1972. TYPE: Peru. Loreto: Iquitos, alt. ca. 100 m, *Killip & Smith 26955* (holotype: US!; isotype: NY!).

Stem 1.0–1.5 cm thick, hemiepiphytic; *scales* of large mature stems mostly 10–15 × 2–5 mm, flaccid, membranaceous, concolorous, whitish to coffee brown or castaneous, spreading or more commonly matted, margins fimbriate, young or terrestrial stems with narrowly lanceolate, castaneous, denticulate scales. *Sterile leaves* up to 1.2 m long; *petiole* up to 21 cm long, about ¼ to ⅓ the length of the lamina; *lamina* to 1 m long, narrowly deltate to elliptic, tapered evenly to the apex, mostly 1-pinnate-pinnatifid, the base occasionally 2-pinnate-pinnatifid, pubescent throughout or rarely glabrous adaxially, rarely with punctate, reddish glands; *pinnae* narrowly triangular, up to 9–19 × 2.5–3.5 cm, serrate to pinnatifid, often with only the lowest pinnae having a few free proximal segments; *pinnules* or *segments* catadromic, slightly falcate, oblong, the basal ones slightly longer than the suprabasal and more deeply cut; *veins* free, 6–9 per segment; *axes* conspicuously pubescent, the hairs 1–2 mm long, unbranched, acicular, whitish, 6–15 celled, the septae often reddish, polyseriate scales lacking, but scales present as reduced, appressed, reddish, flattened, uniseriate "hairs." *Fertile leaves* 2-pinnate, to 0.8 m long, amphiacrostichoid; *axes* pubescent on both surfaces, the hairs ca. 0.1 mm long, colorless, subulate; *proximal pinnae* deeply lobed or fully pinnate, long-caudate; *sporangia* with the capsule walls setose at the apex near the annulus by two hairs, these 1–3 celled; *sporangial stalks* paraphysate; *spores* (44)48–57(63) microns long.

Other illustrations: Martius, Icones Plant. Crypt. Brasil. 87, tab. 25. 1834; von Ettingshausen, Denkschr. Ak. Wien., tab. 7, figs. 3, 10, 11. 1864; Martius, Fl. Brazil, 1(2):586, tab. 38, figs. 1, 2. 1870; Brade, Bradea 1(9): 63, fig. 4; *Ibid.* 67, fig. 7. 1971.

Polybotrya pubens grows primarily in lowland forests of the Amazon basin but occurs in premontane forests up to 1400 m in the Andes (Map 6). During my fieldwork in Ecuador, I found this species in well-drained forest soils that were slightly elevated above the surrounding swamp forest.

This is one of the most distinct species of *Polybotrya*, readily distinguished by its combination of stem scales, lamina shape and cutting,

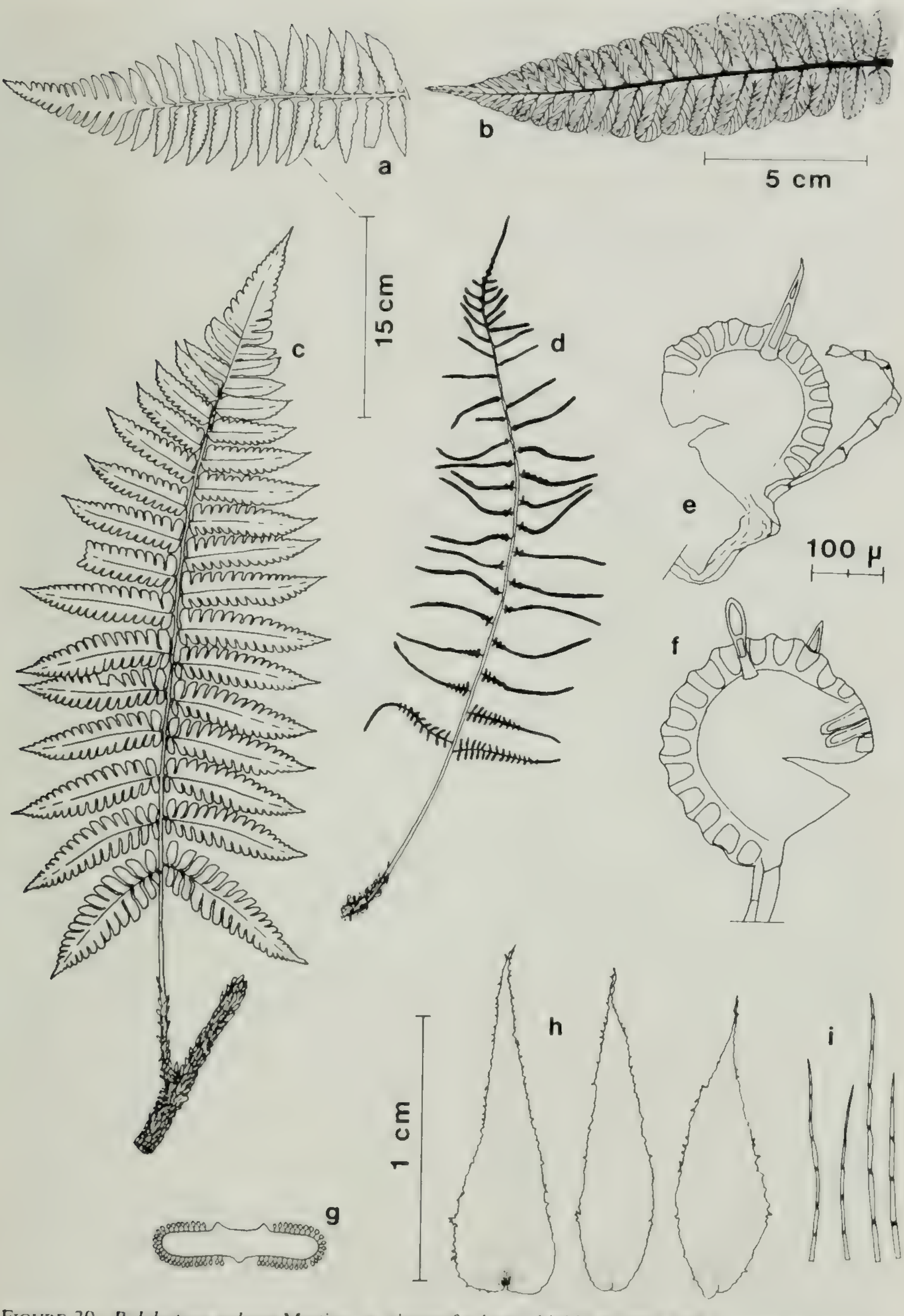

FIGURE 30. *Polybotrya pubens* Martius. a. pinna of a large, highly divided leaf; b. pinna of typically cut leaf; c. sterile leaf; d. fertile leaf; e. setose sporangium with paraphysis on stalk; f. setose sporangium; g. cross section of fertile pinna apex; h. stem scales; i. hairs from sterile lamina. a: *Killip & Smith 26955* (US). b: *Killip & Smith 26543* (NY). c,h,i: *Balslev 4787* (CR). d,g: *Killip & Smith 26194* (NY). e,f: *Holm-Nielsen & Jeppsen 663* (AAU).

pubescence, and long-caudate fertile pinnae. In addition, *P. pubens* has, unlike any other species of *Polybotrya*, setose sporangial capsule walls (Fig. 30e,f). The sterile lamina is usually 1-pinnate-pinnatifid or almost 2-pinnate at the base, but large leaves that are 2-pinnate-pinnatifid for much of their length are occasionally collected (Fig. 30a). These large, more highly divided leaves appear quite distinct but there are intermediate forms between the extremes of lamina cutting. The 2-pinnate-pinnatifid form was named as *P. decorata*.

Polybotrya pubens and *P. glandulosa* might be confused because both have similar laminar cutting, long, acicular hairs, and both grow in lowland forests of the Amazon basin. But the lamina of *P. glandulosa* is, unlike any other species of *Polybotrya*, cuneate and the petiole is extremely short, only 2.5 cm long. Furthermore, its fertile leaf is botryoid instead of amphiacrostichoid, and its sporangial capsules are glabrous instead of setose.

Juvenile stems and thin terrestrial stems have narrow, castaneous, spreading scales that differ from those on the scandent stems. *Dryopteris guentheri* represents a juvenile form of *P. pubens* with this scale type. The transition from juvenile to mature plants and the changes in scale and lamina morphology are shown in an excellent series of specimens collected in Ecuador by Balslev (#4787).

The pubescence of the fertile leaf consists of colorless, subulate hairs about 0.1 mm long—these are much reduced in comparison to the hairs on the sterile leaves. The setae on the sporangial capsule walls are unique in *Polybotrya*. They occur only at the apex of the sporangium near the annulus (Fig. 30e,f); it is odd that these setae are not shown on the sporangia illustrated in 1834 by Martius in his otherwise excellent plate of *P. pubens*. The adaptive value (if any) of the hairs on the capsules is not known.

Unlike all other species of *Polybotrya*, *P. pubens* lacks wide, polyseriate scales on the axes. Rather, scales are present only in their reduced form, that is, as tiny, appressed, reddish, jointed, uniseriate "hairs."

Both Martius and Kunze published the name *P. pubens* in 1834. Kunze's work appeared in the first issue of *Linnaea*, which was published 22–28 June 1834 (Stafleu 1967). Stafleu and Cowan (1981) report that Martius's second fascicle of "*Icones plantarum crytogamicarum*" was published in 1834. Since no month or day is given, I cannot determine which work was published first. I consider Martius the author of *P. pubens* because Kunze clearly attributed this name to Martius.

Specimens examined: COLOMBIA. **Amazonas:** Río Apaporis, Soratama (above mouth Río Kananari) and vicinity, *Schultes & Cabrera 16053* (US).

ECUADOR. **Morona-Santiago:** Taisha, 3–4 km ESE of the military camp, *Brandbyge & Asanza C. 31870* (AAU). **Napo:** Reserva Faunistica Cuyabeno, al lado norte de Laguna Grande, *Balslev 4787* (AAU, CR, Q, QCA), *4802* (AAU, Q, QCA), *Laegaard 51136* (AAU, Q, QCA), *51150* (AAU, Q, QCA), *51224* (AAU, Q, QCA); Parque Nacional Yasuní, in the area of the SEF project, *Øllgaard et al. 38969* (AAU), *39039* (AAU), *39040* (AAU); 6 km along Río Pano, *Holm-Nielsen & Jeppsen 663* (AAU). **Pastaza:** Río Bobonaza, oil exploration camp Chichirota and Destacamento Cabo Pozo, *Øllgaard et al. 34894* (AAU, Q, QCA); Curaray, SE of the airstrip, *Holm-Nielsen et al. 22121* (AAU); oil exploration camp Chichirota, on the Río Bobonaza, *Øllgaard et al. 35350* (AAU); Río Bobonaza, between Cachitama and the outlet of Río Bufeo, *Øllgaard et al. 34703* (AAU). **Santiago-Zamora:** Taisha, *Cazalet & Pennington 7720* (BM, F, K, NY, US).

PERU. **Amazonas:** ridge crest of Quebrada Chuivi (above km 278 of Marañon road), valley of Río Marañon near Cascadas de Mayasi, *Wurdack 1933* (US). **Junín:** E of Quimirí Bridge, near La Merced, *Killip & Smith 23916* (NY, US); Pichis Trail, Santa Rosa, *Killip & Smith 26194* (NY, US); Pichis Trail, San Nicolas, *Killip & Smith 25972* (NY, US); Puerto Bermudez, *Killip & Smith 26543* (NY, US). **Loreto:** above Tamishuyacu, *Croat 19771* (AMAZ, MO); primary forest 17 km SW of Iquitos, *Croat 18508* (MO); Iquitos, ca. 100 m, *Killip & Smith 26955* (NY, US); December 1830, *Poeppig s.n.* (photo of specimen at V, BM); Prov. Maynas, ad Yurimaguas, September 1830, *Poeppig s.n.* (P); La Victoria on the Amazon River, *Williams 3136* (F); lower Río Huallaga, *Williams 4797* (F, US); Yurimaguas, *Spruce 3880* (P, fragment NY); along Quebrada Nawampa, *Croat 17689* (MO); Santa Rosa, lower Río Huallaga below Yurimaguas, *Killip & Smith 28760* (NY, US). **Pasco:** Prov. Oxypampa, Iscoazin, *Foster 7858* (F, USM). **San Martín:** Monte Campana, *Spruce 4740* (photo GH, US); camino a Pushurumbo, 7–8 km al este del Puente de Palo Blanco, Mariscal Caceres, Tocache Nuevo, *J. Schunke 5789* (NY, US); San Roque, *Williams 7620* (F).

BOLIVIA. **La Paz:** Prov. Larecaja, Consata 7 km towards Mapiri, *Beck 4924* (F, LPB); region of Mapiri, San Antonio, *Buchtien 35* (US), *1123* (US), *1124* (NY); region of Mapiri, San Carlos, *Buchtien 260* (UC), *299* (NY); Mapiri, *Rusby 442* (NY).

BRAZIL. **Amazonas:** Rio Negro, 1819, *Martius s.n.* (photo of M specimen at BM). **Pará:** *Martius s.n.* (photo of M specimen at BM).

12. Polybotrya glandulosa Kuhn (Fig. 31, Map 7).

Polybotrya glandulosa Kuhn, Linnaea 36:65. 1869. TYPE: Brazil. Amazonas: San Gabriel, no date, *Spruce s.n.*, not *2116* as indicated on Morton negative, (holotype: B!).

Polybotrya subelliptica Lellinger, Amer. Fern J. 62:56. 1972. TYPE: Peru. Loreto: Mishuyacu, near Iquitos, 100 m, *Klug 1390* (holotype: US!; isotypes: F!, NY).

Stem 1–2 cm thick, hemiepiphytic; *scales* dull brown, thick, opaque, concolorous to bicolorous, curved-appressed, 8–15 × 1.5–2.5 mm, the margins entire, the base thickened and expanded, slightly elevated, the dorsal surface sometimes with a medial groove. *Sterile leaves* up to 75 cm long; *petiole* very short, up to 2.5 cm long; *lamina* 2-pinnate-pinnatifid, subelliptic, 65–73 × 22–28 cm, the base cuneate, about 8 cm wide, the apex long-attenuate, the abaxial surface with or without sessile, red, resinous, round glands, the margins ciliate with hairs similar to those of the veins and axes; *pinnae* ca. 35 pairs, the medial ones 14–16 × 3–3.5(4) cm, sessile or short-stalked, oblong, the base truncate; *pinnules* catadromic, oblong, falcate at the apex, those of the medial pinnae 15–20 × 5–7 mm, the margin entire, crenate or lobed, generally with 6–10 veins, the basal basiscopic margin decurrent; *axes* and *veins* densely pilose on both surfaces, the hairs tawny, pluricellular, acicular, 1.0–2.5 mm long, the scales few or absent. *Fertile leaves* narrowly elliptic, 45 × 15 cm, 2-pinnate-pinnatifid, botryoid; *medial pinnae* 6–8 × 1.5–2 cm; *axes* sparsely pilose, with scattered, linear, appressed, dark scales; *sporangial stalks* paraphysate.

Polybotrya glandulosa, which has been collected only three times, is one of the rarest species of *Polybotrya*. It is the only species in the genus that is endemic to the Amazon basin (Map 7); however, I suspect it will be found in the adjacent Guiana Highlands as that region becomes better explored. I failed to find this species during my fieldwork in the Iquitos area, in part because the location of "Mishuyacu" is unknown. The elevational range for this species is 100–140 m.

This species is unlikely to be confused with any other *Polybotrya* since, unlike other species in the genus, the lamina tapers gradually to an extremely short petiole (Fig. 31c). The long, acicular hairs on the axes and veins further distinguish this species from most other congenerics. *Polybotrya pubens*, however, has long acicular hairs and leaf cutting similar to *P. glandulosa*; since it grows in Amazonian forests, the two species could be confused. *Polybotrya glandulosa*, however, can be distinguished from *P. pubens* because the former has a botryoid, instead of an amphiacrostichoid, fertile leaf and a short petiole.

The specific epithet refers to the red, sessile, round, resinous glands on the abaxial suface of the type specimen (Fig. 31d). The two other collections, however, lack such glands. This variability is not unusual, since glands are variably present in all gland-bearing species of *Polybotrya*.

Specimens examined: VENEZUELA. **Territorial Federal Amazonas:** Dept. Río Negro, 0–3 km N of Cerro de Neblina Base Camp, on the Río Mawarinuma, 140 m, *Liesner 16293* (MO, UC).

PERU. **Loreto:** Mishuyacu, near Iquitos, 100 m, *Klug 1390* (F, NY, US).

BRAZIL. **Amazonas:** São Gabriel, no date, *Spruce s.n.* (B).

13. Polybotrya lechleriana Mettenius (Fig. 32, Map 7).

Polybotrya lechleriana Mettenius, Filices Lechler. 1:4, tab. 1, figs. 1-5. 1854. TYPE: Peru. Puno: San Gavan, *Lechler 2156* (lectotype: B!; isotype: L!; fragments F!, US!; photo GH! of K).

Acrostichum lechlerianum (Mettenius) Hooker, Species Filicum 5:246. 1864, *nom. illeg., non* Mettenius 1856.

Stem to 1.5 cm thick, hemiepiphytic, mucilaginous?; *scales* lanceolate, up to 15 × 3 mm, cream to dull brown, thin, appressed, the margins denticulate to entire. *Sterile leaf* pubescent throughout, the hairs 3–12 celled, 0.3–1.2 mm long, lax, spreading, colorless; *petiole* ⅓–½ as long as the lamina, stramineous; *lamina* finely divided, (4)3-pinnate-pinnatisect, lanceolate, both surfaces pubescent, especially along the axes and veins, eglandular, the apex acute, not long-attenuate; *pinnae* lanceolate to ovate, (7)10–15 × (2)3–7(12) cm, the base truncate, short-stalked, crowding the rhachis; *pinnules* catadromic, oblong with subparallel sides, the base truncate, nearly sessile, crowding the costa, the apex acute to rounded; *ultimate segments* single veined, falcate, 0.5–1 mm wide; *axes* pubescent abaxially, usually with a single scale at the juncture of the costa and

FIGURE 31. *Polybotrya glandulosa* Kuhn. a. stem scales; b. fertile leaf; c. sterile leaf; d. abaxial surface of sterile pinna showing sessile reddish glands (as dots) and acicular hairs; e. medial pinna a–c,e: *Klug 1390* (US, F). d: *Spruce s.n.* (B).

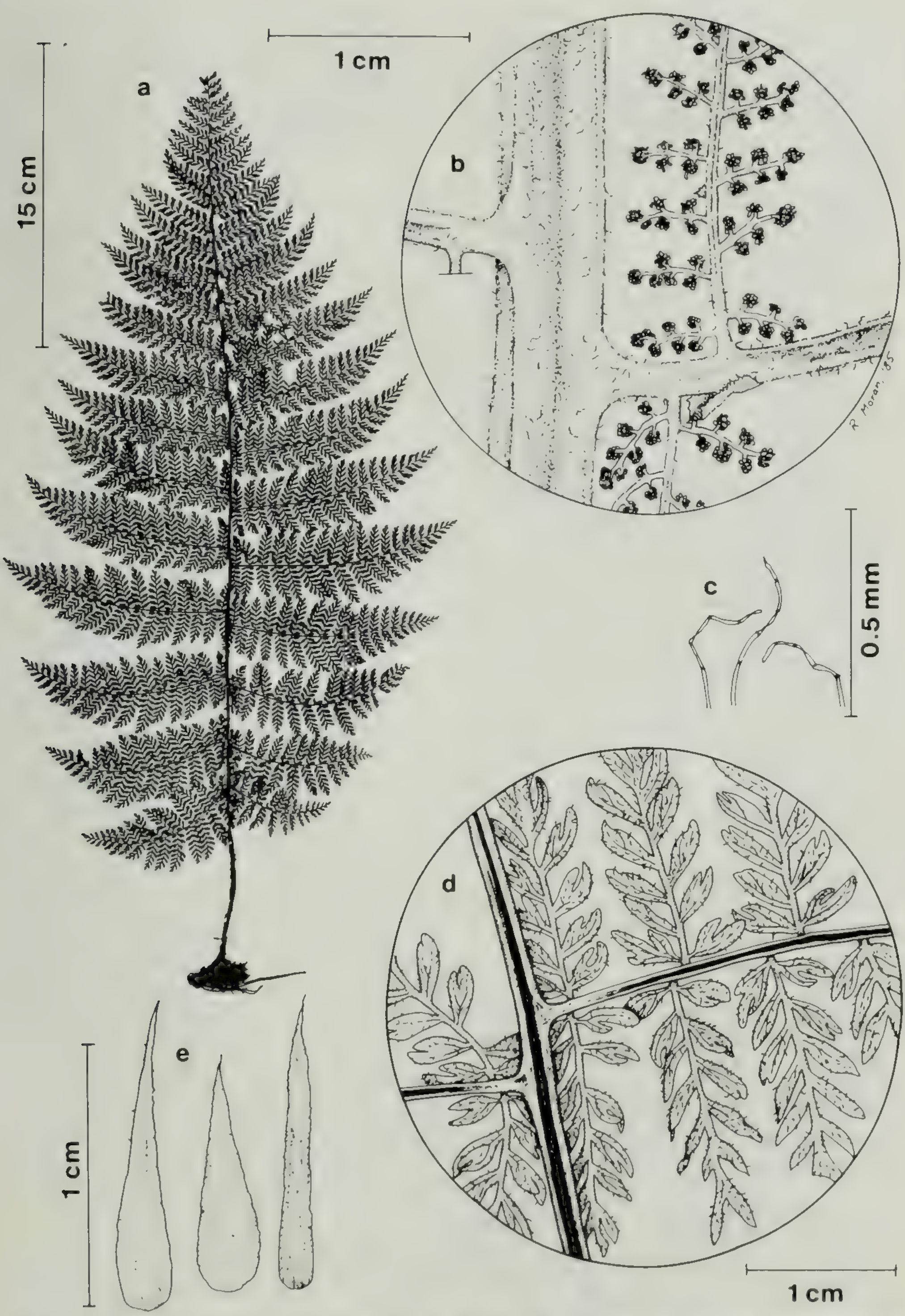

FIGURE 32. *Polybotrya lechleriana* Mettenius. a. sterile leaf; b. rhachis-costa juncture of fertile leaf; c. costal hairs; d. rhachis-costa juncture of sterile leaf; e. stem scales. a,c: *Spruce 4744* (P). b,d: *Stübel 914* (B). e: *Dudley 10325* (GH).

costule, the scale ovate, appressed, thin, brown; *grooves* glabrous or puberulent within, truncated by the ridges of the next lower order, usually becoming shallower near the juncture. *Fertile leaf* 3-4-pinnate, botryoid, pubescent with hairs like those on the sterile leaf; *sori* distinct, round, 0.5–0.8 mm wide, on short stalks, these 1–2 mm long, the receptacle moundlike; *sporangial stalks* paraphysate; *spores* (50)54–60(65) microns long.

Other illustrations: Hooker, Second Century of Ferns, tab. 97. 1861; Mettenius's original description has an excellent illustration of the type at Berlin.

Polybotrya lechleriana occurs in rich montane forests from (100)1000–1500 m. This species is primarily Andean but has a notable range disjunction in the Guiana Highlands at Mt. Roraima in Guyana, 1900 km from the nearest known population in Colombia (Map 7). This disjunction is best explained as an example of long distance spore dispersal. Another significant Andean–Guianan range disjunction occurs in *P. fractiserialis* (Map 3).

This species is easily recognized by its finely divided sterile lamina with very narrow, single-veined segments and lobes (Fig. 32). The finely cut leaves, so unlike others in the genus, are probably what prompted Copeland (1947) to remark that this species "looks out of place here [in *Polybotrya*]." But *P. lechleriana* has all the features of a typical *Polybotrya* including the unique stem anatomy of the genus.

Some forms of this plant resemble *Polybotrya stolzei* an endemic to the Andes of Colombia, but *P. lechleriana* differs by the narrower width of its ultimate segments or lobes, each of which is one-veined (see key). *Polybotrya lechleriana* probably evolved from a less dissected ancestor in the *P. alfredii* group by cessation of the growth of the marginal meristem to produce a more finely divided sterile lamina. This species is named in honor of Wilibald Lechler (1814–1856), a German pharmacist, botanist, and explorer, who sent many of his collections to Mettenius.

Specimens examined: GUYANA. Mt. Roraima, Waruma Trail, *Persaud 114* (NY).

COLOMBIA. **Cauca:** forests of Río Timbiqui, *Lehmann B.T413* (GH). **Chocó:** alrededores de San José del Palmar, Cerro S de la población, *Forero & Jaramillo 2469* (COL, MO, NY); NW side of Alto del Buey, *Lellinger & de la Sota 281* (COL, US); Río Nuqui, *Haught 5498* (COL, F, NY, US). **Nariño:** Municipio de Altaquer, entre Junín y Buenavista, 650 m, *Mora 4287* (COL).

ECUADOR. **Chimborazo:** Río Palora, eastern cordillera of Riobamba, 1400 m, *Rimbach 31* (GH, PH, US). **Pastaza:** Mera, remnants of primary forest in hills above town, *Plowman & Davis 4542* (GH). **Tungurahua:** along road between Puyo and Baños at second bridge W of Mera, ca. 3 km W of Mera, 1160 m, *Croat 49718* (MO, UC); Baños–Pintuc, *Stübel 913a, 914* (B, BM).

PERU. **Cuzco:** Prov. La Convención, Cordillera Vilcabamba, Camp 2.5, 1760 m, 73°38′W, 12°38′S, *Dudley 10325* (GH); Paucartambo, Valle de Pillahuata, *Gerrera 1624* (US). **Junín:** Prov. Satipo, "Mapiri" ca. 12 km SW of Chequitavo, *A.C. Smith 61713* (MO, USM); Pichis Trail, Porvenir, 1500–1900 m, *Killip & Smith 25921* (NY, US). **Puno:** San Gavan, *Lechler 2156* (B, F, GH, L, US), *2176* (B); La Pampa, Río Tavara, *Watkins s.n.* (US). **San Martín:** in monte Guayrapurima, prope Tarapoto, *Spruce 4744* (L, P; fragment US). **Dept. unknown:** entre Los Ríos Tintiuiguiato del Pachiri y Tapecia del Tocate, 1500 m, *Bues 1743* (US).

BOLIVIA. **La Paz:** Hacienda Simaco sobre el camino a Tipuani–Tale, 1400 m, *Buchtien 5308* (BM, GH, MO, NY, UC, US, Z).

14. Polybotrya attenuata Moran, *sp. nov.* (Fig. 33, Map 7).

Polybotrya attenuata Moran, *sp. nov.* TYPE: Colombia. Antioquia: Guatape, forests on slopes above river, 1/77, *McAlpin & Kuhn 77-12* (holotype: NY!). The plant from which the type specimen was taken is cultivated in the fern greenhouse, New York Botanical Garden (accession no. 332/78).

Planta hemiepiphytica; caulis ca. 1 cm diam.; squamulis membranaceis, linearibus, acutis, 9–12 mm longis, 0.3–0.7 mm latis, in margine denticulatis vel integris; laminae steriles lanceolatae vel anguste deltatae, 3-pinnatae, apice longiattenuatae, usque ad 55 cm longae, 26 cm latae, glabrae vel punctatae, glandulis resinaceis, rotundis; pinnulae catadromicae, 2.0–2.5 cm longae, 0.8–1.2 cm latae, apice rotundatae; segmenta tertiaria obovata, ad basim cuneata; costae et rhachides sulcatae pubescentes in sulco, squamis angustis, fuscatis, denticulatis; folia fertilia botryoidea; sori rotundi, ca. 1 mm longi, pedicellati.

Stem about 1 cm wide, hemiepiphytic; *scales* light to dark brown, mostly concolorous or rarely with a narrow hyaline border, thin, linear, 9–12 × 0.3–0.7 mm, the margins subentire to denticulate. *Sterile leaf* up to 0.8 m long; *petiole* ⅓–¼ as long as the lamina; *lamina* to 55 × 26 cm, 3-pinnate, narrowly lanceolate or triangular, the apex long-attenuate, the tissue with or without

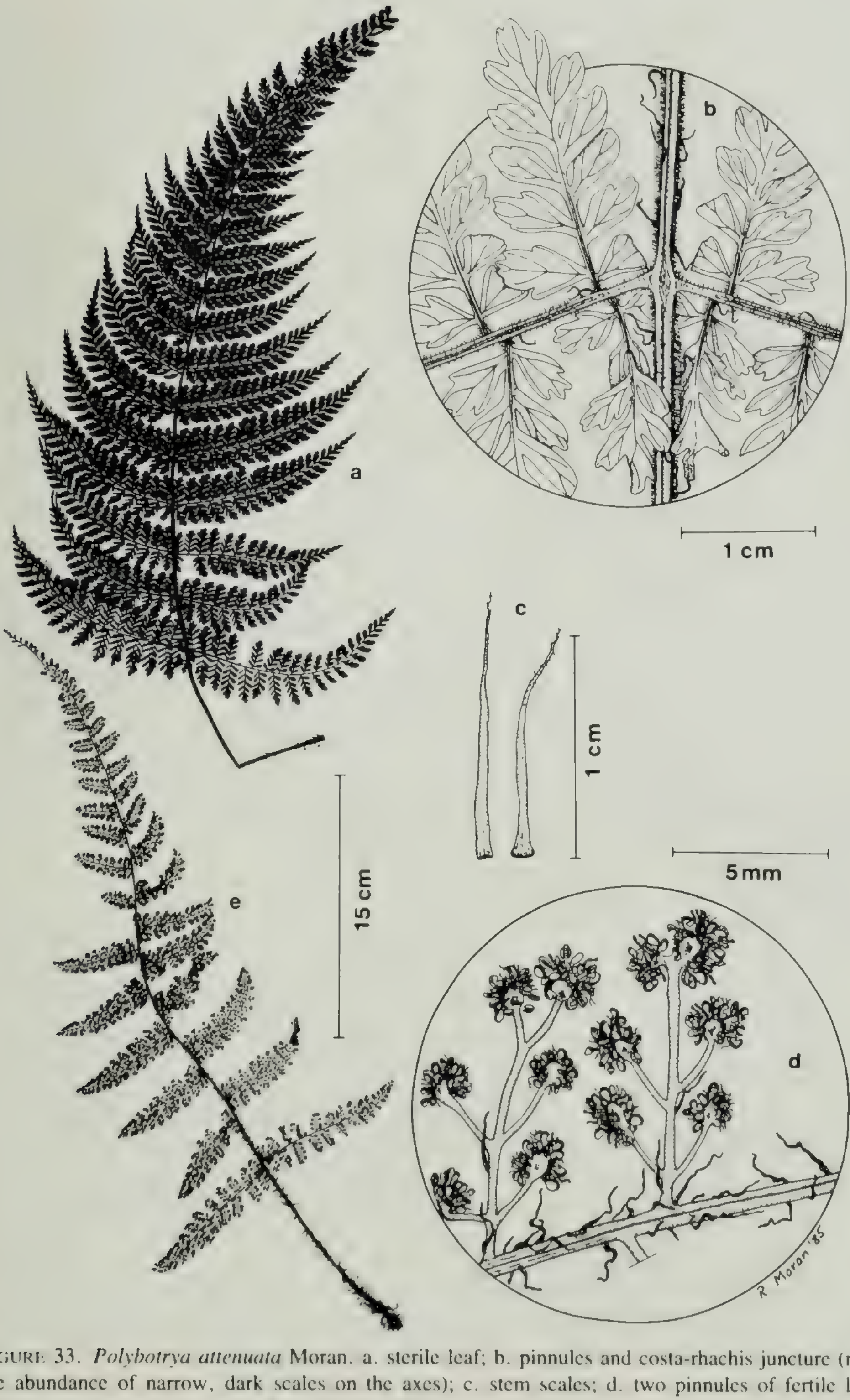

FIGURE 33. *Polybotrya attenuata* Moran. a. sterile leaf; b. pinnules and costa-rhachis juncture (note the abundance of narrow, dark scales on the axes); c. stem scales; d. two pinnules of fertile leaf; e. fertile leaf. a–e: *McAlpin & Kuhn 77-12* (NY).

punctate, resinous, spherical, sessile glands; *pinnae* 10–13 × 3.5–4.0 cm long, lanceolate to oblong, the base truncate, short-stalked, crowding the rhachis; *pinnules* catadromic, 2.0–2.5 × 0.8–1.2 cm, with only 5–7 lobes or segments, the apex acute or rounded, the base truncate, sessile or with a short stalk less than 1 mm long; *tertiary segments* obovate, entire to slightly lobed, containing several vein branches, the base cuneate; *axes* pubescent within grooves and especially abaxially, the hairs 4–12 celled, 0.2–0.3 mm long jointed, with reddish cross-walls; *costal scales* numerous, narrow, dark, denticulate, tortuous, appressed; *grooves* pubescent within, the hairs reddish, multicellular. *Fertile leaves* botryoid, 3-pinnate, densely scaly, the scales grading into jointed hairs (the hairs are actually reduced scales); *sori* stipitate, the stalks 1–3 mm long; *sporangial stalks* paraphysate.

Polybotrya attenuata, named for its distinctive, long-attenuate leaf apices, is endemic to the Andes of Colombia (Map 7). This species differs from *P. lechleriana*, a similar species, by its long-attenuate apex, oval tertiary segments, resinous glands on the lamina, and the darker, narrower scales on the axes. The pinnules, furthermore, are shorter and stubbier, having only 5–7 lobes and/or segments, and these have a cuneate base (Fig. 33a,b).

The presence of glands on the lamina is not constant. The living plant from which the holotype was made has always produced leaves having round, sessile, resinous glands on the undersurface. The Lehmann specimen, however, lacks such glands. Similar glands are also variably present in other species, such as *P. osmundacea* and *P. glandulosa*.

Specimens examined: COLOMBIA. **Antioquia:** Guatape, *McAlpin & Kuhn 77-12* (NY). **Nariño:** along river Pipulquer, west slopes of the western Andes, *Lehmann 500B* (US).

15. Polybotrya stolzei Moran, *sp. nov.* (Fig. 34, Map 9).

Polybotrya stolzei Moran, *sp. nov.* TYPE: Colombia. El Valle: Santa Rosa, Dagua Valley, forest along Río Cabellete, 200–300 m, 22 September 1922, *Killip 11549* (holotype: US!; isotypes: GH!, NY!, PH!).

Planta hemiepiphytica; caulis 0.6–1.5 cm diam., (mucilaginus?); squamae fuscatae, opacae, lineares, integrae, usque ad 12 mm longae, 0.4 mm latae; lamina sterilis 3-pinnata, plerumque pubescens in superficiebus ambabus; rhachis et costae pubescentes, squamis ovatis tenuibus aliquot; pinnulae catadromicae, pro parte maxima sessiles, usque ad 33 × 9 cm; segmenta tertiaria ovalia vel oblonga integra, (5)6–8(10) × (2)3–4(5) mm. Folia fertilia ignota.

Stem 0.6–1.5 cm thick, hemiepiphytic, mucilaginous (?); *scales* dull brown, appressed, opaque, linear, 0.4–12.1 × 0.3–1.0 mm, margins subentire. *Sterile leaves* up to 1 m long; *petiole* ¼ to ½ as long as the lamina; *lamina* lanceolate or subdeltate, 30–65(80) × 19–32(60) cm, 3-pinnate, usually pubescent on both surfaces, always so along the veins beneath, the hairs whitish to tawny, articulated, 0.1–0.4 mm long, spreading; *pinnae* to 33 × 9 cm, narrowly triangular to lanceolate, equilateral or, in the basal pair, with the basiscopic side slightly prolonged, the base truncate, short-stalked, crowding the rhachis; *pinnules* catadromic, oblong, the base truncate, nearly sessile, the apex rounded to acute; *tertiary segments* ovate to oblong, (5)6–8(10) × (2)4(5) mm, with several vein branches, the margins entire to slightly lobed; *axes* pubescent abaxially, with a few thin, ovate, brown scales, especially at the pinnule junctures; *grooves* nearly glabrous to moderately puberulent within, never packed with long-protruding hairs, truncated by the ridges of the next lower order. *Fertile leaf* unknown.

This new species is named for Robert G. Stolze, pteridologist at the Field Museum of Natural History, Chicago, Illinois. He originally suggested this genus to me and has given much help and encouragement during the preparation of this monograph.

Polybotrya stolzei is endemic to the western Andes of Colombia (Map 9), occurring in wet, shaded forests from 200–1750 m. The laminar cutting of *P. stolzei* is intermediate between *P. lechleriana* and *P. alfredii*. Extremely large pinnules of *P. stolzei* look like those of *P. alfredii* but are distinguished by the pubescence on both surfaces of the lamina and by the blunter apices of the medial pinnules. Smaller, more delicate forms of *P. stolzei* may look like *P. lechleriana* but are distinguished by their oblong tertiary segments with more than one vein per segment. Un-

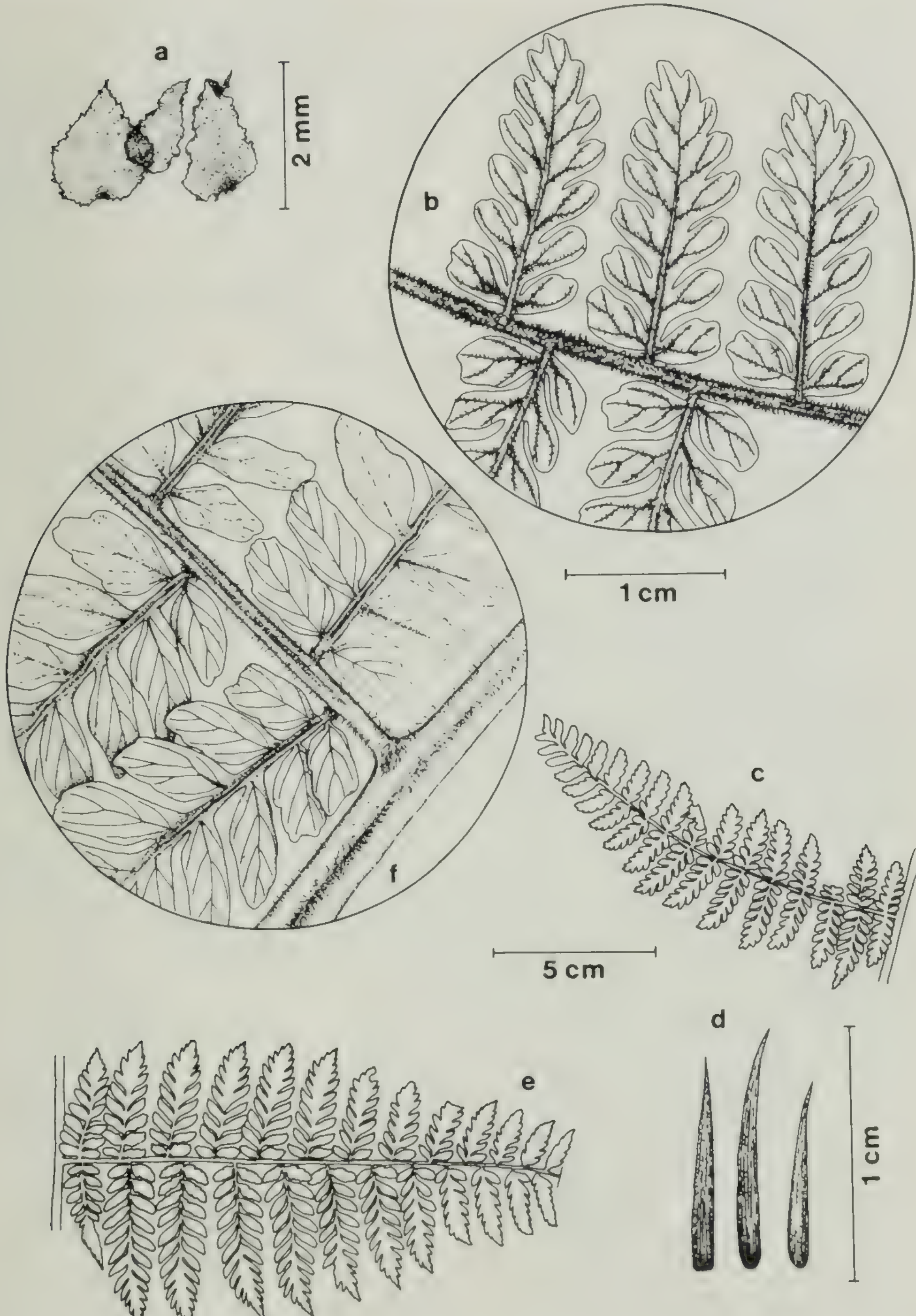

FIGURE 34. *Polybotrya stolzei* Moran. a. costal scales from the pinnule-costa junctures; b. abaxial view of medial pinnules of "c"; c. medial pinna; d. stem scales; e. basal pinna of large leaf; f. adaxial view of rhachis-costa juncture. a-d: *Killip 11549* (GH). e,f: *Lellinger & de la Sota 284* (COL).

fortunately, none of the collections contain fertile leaves and this structure, therefore, cannot be compared to the distinctive botryoid fertile leaf of *P. lechleriana*.

Specimens examined: COLOMBIA. **Chocó:** NW side of Alto del Buey, *Lellinger & de la Sota 280* (COL, US), *284* (COL, US); principal ridge and slopes 2 km E of San José del Palmar, 1550–1600 m, *Lellinger & de la Sota 747* (COL, LP, US), *748* (COL, LP, US). **El Valle:** Santa Rosa, Dagua Valley, forest along Río Caballete, 200–300 m, *Killip 11549* (GH, NY, PH, US).

16. Polybotrya alfredii Brade (Fig. 35, Map 8).

Polybotrya alfredii Brade, Bradea 1:12, tab. 1, fig. 2. 1969. TYPE: Costa Rica. San José: Tablazo, 1900 m, July 1908, (Brade's original description states August, apparently an error.) *Brade & Brade 98* (holotype: HB; isotype: NY!).

Polybotrya alfredii Brade f. *carpinterae* Brade, Bradea 1:13. 1969. TYPE: Costa Rica. San José: Carpintera, terrestrial, 1500 m, 25 November 1908, *Brade & Brade s.n.* (holotype: HB).

Polybotrya gracilis Brade, Bradea, 1:14, tab. 1, fig. 3. 1969. TYPE: Costa Rica. Cartago: Tablazo, 1900 m, 28 August 1908, *Brade 554* (holotype: HB).

Stem 1–2 cm wide, hemiepiphytic, the apex in living plants usually covered by a thick mucilage that disappears upon drying; *scales* dull, dark to light brown, opaque to translucent, 8–16(22) × 1–1.5(2.0) mm wide, narrowly lanceolate, spreading, attached across the width of the slightly thickened base, the margin denticulate or more commonly entire. *Sterile leaves* up to 1.4 m × 0.7 m; *petiole* up to 35 cm long; *lamina* ovate, up to 3-pinnate-pinnatifid, subchartaceous, often drying greyish green, the proximal margins of the pinnule bases often ciliate, the hairs less than 0.1 mm long; *pinnae* up to 45 × 22 cm, apex acuminate; *pinnules* up to 12 × 5 cm, ovate to narrowly triangular, the base truncate and symmetrical, those of the basal pinnae anadromic or subequal, those of the medial pinnae catadromous; *ultimate segments* ovate to oblong, entire, crenulate, serrate or lobed, the apex obtuse or acute; *axes* evenly pilosulous abaxially, the hairs 0.1–0.2 mm long, usually tawny; *grooves* pubescent within, very shallow or even disappearing within about 1 cm of the rhachis so that the costa is almost terete where it joins the rhachis. *Fertile leaves* up to 0.8 × 0.35 m, up to 3-pinnate-pinnatifid, ovate, coenosoric; *axes* pubescent, the hairs short, 0.1–0.2 mm long, usually with ovate to lanceolate, appressed, thin, denticulate to fimbriate scales; *sporangial stalks* paraphysate; *spores* (50)55–62(66) microns long.

Other illustrations: See the original descriptions cited above.

The altitudinal range of *Polybotrya alfredii* is 700–1900 m. In Ecuador, this species grows in rich montane forests in the eastern Andes. In Costa Rica, this species occurs primarily in wet, shaded cloud forests, usually growing alongside *P. gomezii*. *Polybotrya alfredii* produces numerous terrestrial leaves that often predominate the forest floor. Twice in Costa Rica and once in Ecuador, I saw fertile leaves produced from the terrestrial portion of the stem. These are the only instances in which I saw fertile leaves produced terrestrially by a scandent species.

Polybotrya alfredii looks like *P. lourteigiana* but can be distinguished by its more highly cut lamina. Since leaves lower on the stem tend to be smaller and less divided than those higher on the stem, cutting should be compared using pinnae over 25 cm long (see couplet 24 in the key). The two species also differ in the shape of the ultimate segments or lobes; *P. alfredii* has relatively more ovate and shorter segments than *P. lourteigiana* (compare Figs. 35 & 37).

Unlike all other species of *Polybotrya*, *P. alfredii* has the stem apex and the lowermost 5 to 15 cm of the petiole covered with a thick, translucent mucilage. Mucilage is totally lost upon drying and therefore not visible on herbarium specimens. The function of this mucilage is unknown. More fieldwork is needed to determine if this unusual mucilage occurs in two closely related species, *P. lechleriana* and *P. lourteigiana*. Nectaries are another unusual feature of the morphology of *P. alfredii*. During fieldwork in Costa Rica, I saw nectaries on the rhachis of *P. alfredii* like those described by Koptur et al. (1982) for *P. osmundacea*. See the Morphology and Anatomy section of this monograph for further information concerning nectaries.

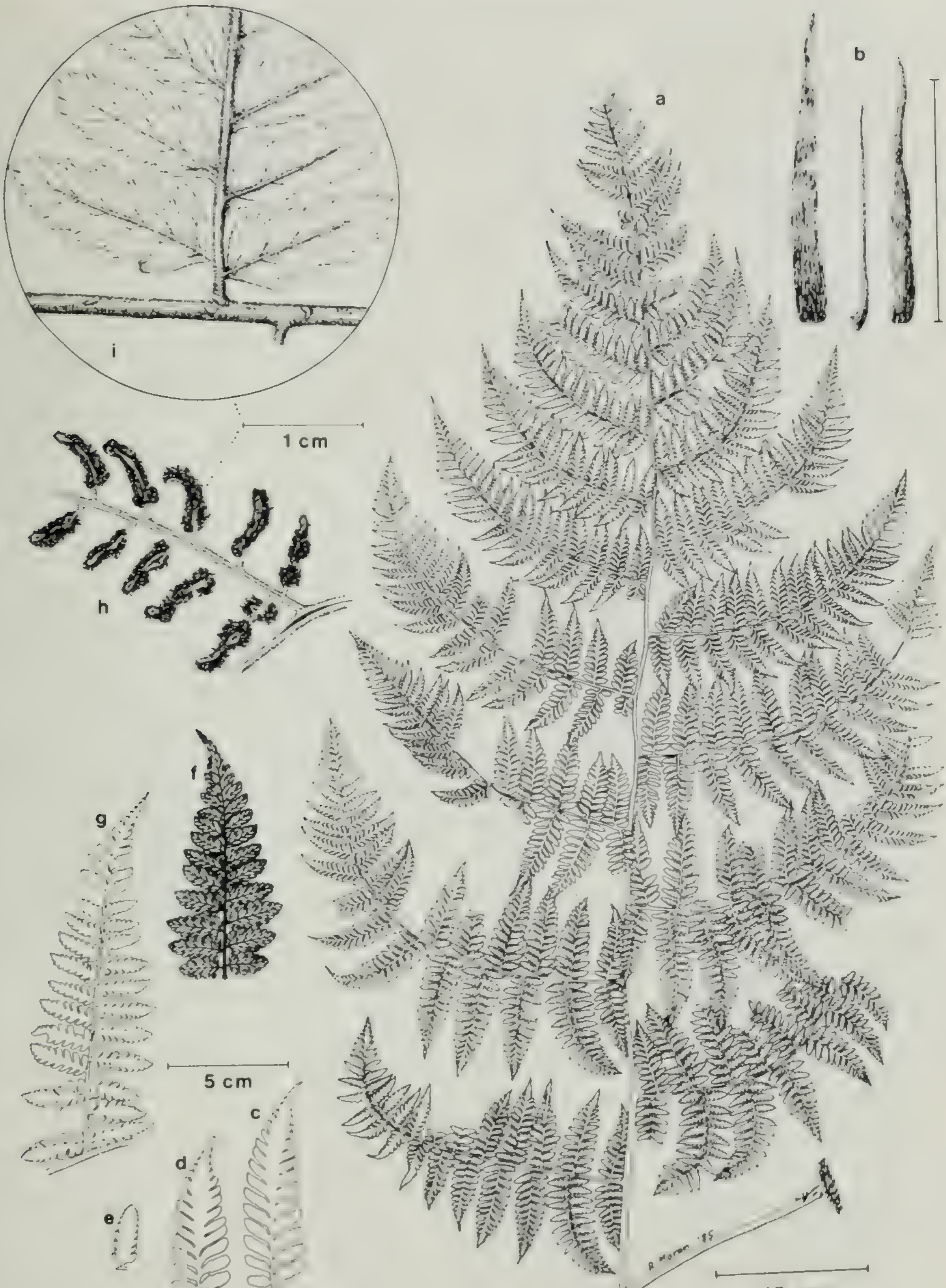

FIGURE 35. *Polybotrya alfredii* Brade. a. sterile leaf; b. stem scales, the middle shown sideways; c–g. pinnules, acroscopic side to the right; h. fertile pinnule, adaxial view; i. adaxial surface of costa and pinnule base. a,b,f,h,i: *Moran 2442* (CR). c: *Moran 3532* (F). d: *Buchtien 5164* (US). e: *Moran 3214* (CR). g: *Dwyer 8337* (MO).

I put *P. gracilis* in synonymy with *P. alfredii*, although the former appears distinct because the leaf is smaller, only 2-pinnate, and has obtuse pinnule apices (Fig. 35e). *Polybotrya gracilis* resembles *P. alfredii*, however, in such characteristics as scales, pubescence, stem mucilage, habitat, and range. Furthermore, at several localities in Costa Rica, I collected plants that exhibited complete intergradation between the typical large leaves of *P. alfredii* and the smaller ones of *P. gracilis*. *Polybotrya gracilis*, therefore, represents a small-leaf form of *P. alfredii* that has well-rounded pinnule apices. I chose the name *P. alfredii* over *P. gracilis* because an isotype has been seen. This species is named in honor of Alexander Brade's brother and field companion, Alfred Brade.

Specimens examined: NICARAGUA. **Rivas:** Isla de Ometepe, NW slope of Volcán Maderas, *Stevens & Krukoff 6518* (CR); Graytown, Camp Murroeal, *Shimek & Smith s.n.* (MICH).

COSTA RICA. **Alajuela:** Univ. of San Ramón biological field station, *Moran 3214* (CR, F, GH, MO); 12 km NNW of San Ramón by road on way to San Lorenzo, 1 km S of Balsa, *Liesner & Judziewicz 14855* (CR, MO); San Jerónimo, *Wercklé 559* (US); Suerre, llanuras de Santa Clara, *Donnell Smith 6939* (US); Santa Clara, *Cooper 10240* (US); NW of Zarcero, ca. 2 km W of Zapote on dirt road to Sta. Elena, *Lellinger & White 1361* (US); San Antonio de Zarcero, *A.C. Smith 48/293* (US); N of San Ramón, ca. 4 km N of Balsa along road to Colonia Palmerena, *Lellinger & White 1244* (US); Santiago de San Ramón, *Brenes 21980* (F), *14248* (GH); Alto de la Palma de San Ramón, *Brenes 11676* (F, NY); 7 miles N of San Ramón square along ridge road, *Evans & Bowers 2944* (MO); Finca La Selva, San Rafael de Vara Blanca, pendiente N del Volcán Barba, *Jiménez 803* (F); vicinity of La Palma, *Maxon 412* (NY); 11 km N of San Ramón, *Mickel 2958* (LP, NY, UC); San Luis de Zarcero, *A.C. Smith 778* (NY). **Cartago:** road between La Suiza and Tuis, *DeWolf 385* (CR); Pacayas, *Lankester 653* (US); along Inter-American Hwy. between Cartago and San Isidro del General, *Scamman 5985* (CR), *5986* (CR); Orosi, Finca del Sr. Valverde, *Brade 16824* (CR); El Muñeco, S of Navarro, *Standley 33648* (US); Santa Clara de Cartago, *Maxon & Harvey 8242* (US); SE of Platanillo, along Camino Raiz de Hule, *Croat 36761* (MO); Platanillo, *de la Sota 5252* (LP, US); foot of Volcán Turrialba, Pacayas, *Scamman 7155* (CR); along road from Moravia to Quebrada Platanillo (Tsipiri), *Croat 36669* (MO); ca. 22 km E of Turrialba, high ridge above Platanillo, *Mickel 3426* (LP, NY); near the town of Estrella, *Moran 2237* (CR), *2241* (CR); near Alto Patillos, *Moran 2442* (CR); Reserva e Tapantí, *Gómez 18906* (CR, MO, UC); Tapantí, *Grayum & Sleeper 3448* (MO); 12–16 km S of Tapantí, along the road above the Río Grande de Orosi, *Stolze 1488* (F, UC). **Heredia:** 7.5 km N of Vara Blanca, in vicinity of Río La Paz Grande, *Croat 36007* (MO); Vara Blanca de Sarapiquí, N slope of Central Cordillera, *Skutch 3236* (GH, US); Santo Domingo de Vara Blanca, *Valerio 2356* (US); Vara Blanca, between Volcán Poas and Barba, *Chrysler & Roever 5095* (US); 4 km N of Vara Blanca, *Croat 35608* (MO); near Río Las Vueltas, NE of Volcán Barba, *Lent 2642* (F); Virgen del Socorro, *Moran 3168* (CR). **Puntarenas:** 5 km NE Finca las Cruces, San Vito de Java, *Burch 4505* (NY); near field station, Rincón de Osa, *Burch 4414* (NY); 5 km S of San Vito de Java, in vicinity of biological field station at Wilson finca, *Mickel 2003* (NY); 5 km S of San Vito de Java, 1–4 km SW of biological station at Finca Wilson, *Mickel 3126* (NY). **San José:** Tablazo, *Valerio 63* (US); *Biolley 73* (US, Z); Tablazo, *Brade & Brade 67* (P), *98* (NY); Alto La Palma, *Moran 2325* (CR).

PANAMA. **Chiriquí:** Palo Alto, just E of Boquete, *Stern et al. 1034* (CR, US); Holcomb trail, *Cornman 927* (MICH, UC, US); vicinity of El Boquete, *Cornman 1178* (US), *1233* (US), *Maurice 699* (US); Río Caldera, from El Boquete to the Cordillera, *Killip 5202* (CR, US); valley of Río Piamasta, about 5 mi E of Boquete, *Killip 5163* (US), *5386* (US), *5429* (CR, MICH, US). **Coclé:** Valle de Antón, *Ocampo 877* (CR); Cerro Pilon, *Dwyer 8337* (MO); cloud forest at La Mesa above El Valle, *Croat 13431* (MO, UC).

ECUADOR. **Napo:** camino Baeza–Tena, 15 km al norte de Tena, 1100 m, *Moran 3532* (F, GH, PORT, Q, QCA). **Pastaza:** village of Río Chico, 8 km from Puyo, *Shemluck 304* (F). **Tungurahua:** casi 25 km al este de Baños, detras el pueblo Río Negro, por Río Topo (malempresado "Río Toro" en el mapa), *Moran 3570* (F, GH, Q, QCA).

PERU. **Huánuco:** SW slope of the Río Llulla Pichis watershed on the ascent of Cerro del Sira, *Dudley 13258* (GH), *18265A* (GH).

BOLIVIA. **La Paz:** Hacienda Simaco sobre el camino a Tipuana, *Buchtien 5164* (GH, US).

17. Polybotrya botryoides (Baker) C. Chr. (Fig. 36, Map 8).

Polybotrya botryoides (Baker) C. Chr., Index Filicum 504. 1906.

Acrostichum botryoides Baker, J. Bot. 19:206. 1881. TYPE: Colombia. Antioquia: on trees in the forest, 6000–7000 ft, 22 July 1880, *Kalbreyer 1873* (holotype: K; photo and fragment GH!, US!).

Stem to 2 cm thick, hemiepiphytic; *scales* dull brown, about 1 cm long, with the margins subentire to erose, the base curved and thickened. *Sterile leaves* up to 1.5 m (?); *petiole* densely scaly at

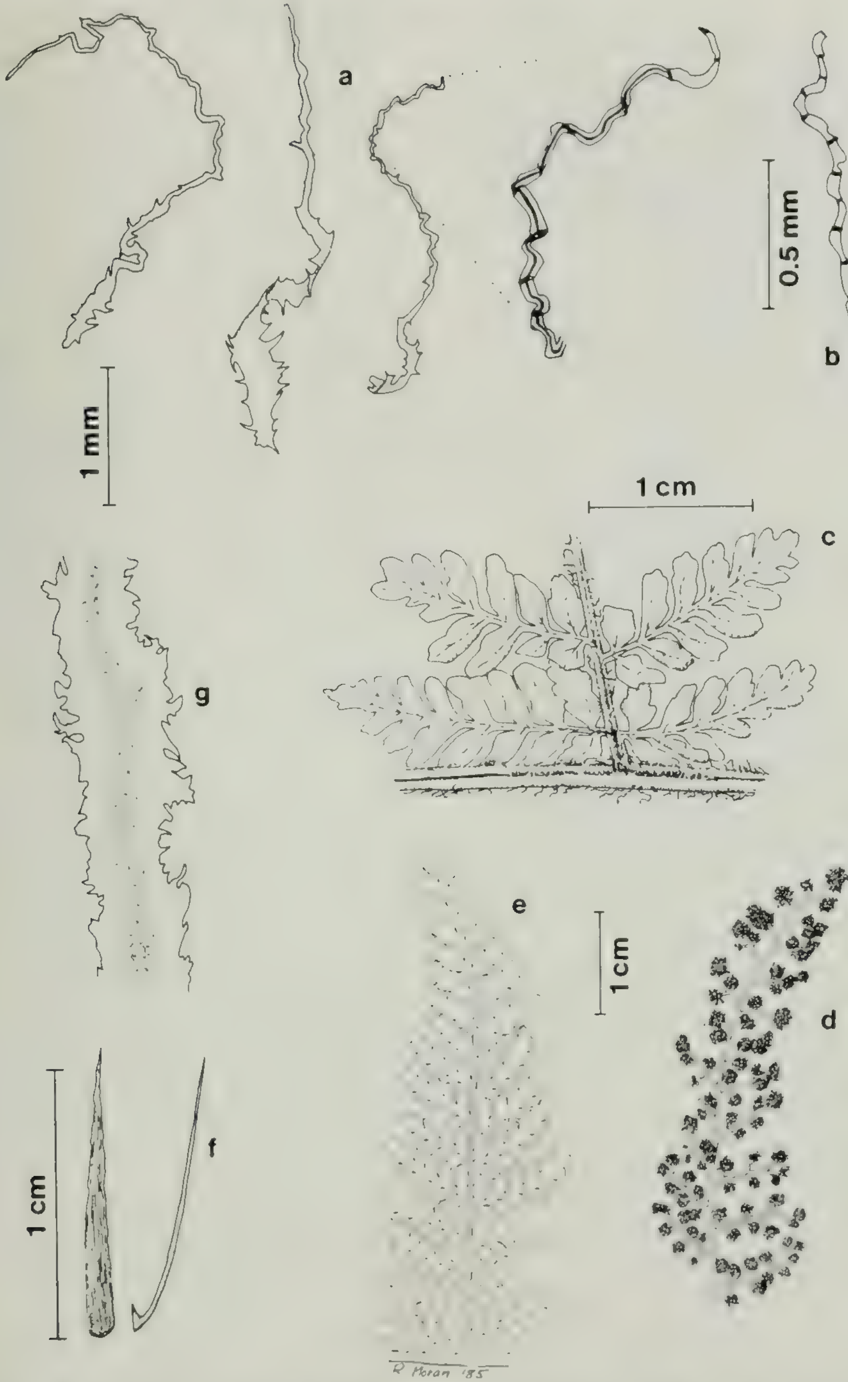

FIGURE 36. *Polybotrya botryoides* (Baker) C. Chr. a. costal scales, the one on the right enlarged to show the biseriate apex; b. uniseriate "hair" from the costa. Such hairs are actually reduced scales as shown by their intergradation with the scales and by their characteristics which differ from those of true hairs; c. sterile pinnule base; d. botryoid fertile pinnule; e. sterile pinnule; f. stem scale, at right is a side view showing the thickened base; g. petiolar scale, medial portion darkened and margins erose. a–g: *Juncosa 1369* (MO).

base, the scales similar to those on the stem, but with wider pale borders and more strongly erose; *lamina* 4-pinnate, nearly glabrous on both surfaces; *pinnae* lanceolate, up to 35 × 20 cm, finely divided all the way to the apex; *pinnules* up to 10 × 3 cm, catadromic or subequal, lanceolate, the base often overlapping the costa, subequilateral, i.e., not prolonged acroscopically, short-stalked (1–2 mm long); *tertiary segments* oblong, sessile, up to 2 × 0.9 cm, apex acute or rounded, base equilateral; *quaternary segments* oblong to ovate, sessile, up to 5 × 3 mm, the margins entire or crenate; *axes* scaly, the scales numerous, tortuous, thin, reddish, most of these only 2–5 cells wide, intergrading with hairs, these articulate, reddish, 4–8 celled, 0.1–0.3 mm long; *grooves* pubescent within by reddish hairs. *Fertile leaves* botryoid, 3-4-pinnate, with the ultimate soriferous segments globose, 1–2 mm diameter; *receptacle* paraphysate by articulate hairs, these often buried among the sporangia; *sporangial stalks* paraphysate; *spore size* unknown.

Polybotrya botryoides is endemic to the Andes of Colombia (Map 8), occurring in forests from 1830–2130 m. The above description is based primarily on the Juncosa collection, which was the only dried specimen I had available for study. I could not find enough spores on this specimen to make an adequate measurement of spore size.

This rare species can be separated from all other species of *Polybotrya* by its distinctive combination of botryoid fertile leaf, 4-pinnate sterile leaf, and axes covered by numerous, linear, tortuous, reddish scales (Fig. 36a). No other species of *Polybotrya* is as finely divided as this one. *Polybotrya botryoides* looks like *P. alfredii* because of its large decompound lamina, catadromically arranged pinnules, subequal pinnule bases, pubescence of the axes, and dull brown stem scales. The Venezuelan endemic *P. canaliculata* also has botryoid fertile leaves, but it lacks hairs on the axes, has very different axial scales, and is less finely cut (Fig. 52).

Specimens examined: COLOMBIA. **Antioquia:** *Kalbreyer 1873* (photo and fragment GH, US); main hwy. Medellín–Puerto Triunfo, Municipality Cocorna, ca. 5 km E of Cocorna Peaje, Quebrada El Biadal, 1830 m, *Juncosa 1369* (MO, UC).

18. Polybotrya lourteigiana Lellinger (Fig. 37, Map 10).

Polybotrya lourteigiana Lellinger, Proc. Biol. Soc. Washington 89:723, fig. 5. 1977. TYPE: Colombia. Chocó: Trail along ridge from the confluence of the forks of the Rìo Mutatá above the Río Dos Bocas to the top of Alto del Buey, ca. 1450–1750 m, *Lellinger & de la Sota 251* (holotype: US!; isotypes: COL!, LP!).

Stem to 2 cm thick, hemiepiphytic, mucilaginous (?); *scales* dark brown, concolorous, and entire, or cream-colored with a darker center and ciliate margins, mostly 8–17 × 0.5–2.0 mm. *Sterile leaves* up to 1.6 m long; *petiole* up to ½ as long as the lamina; *lamina* glabrous on both surfaces, up to 3-pinnate but mostly 2-pinnate-pinnatifid throughout, deltate to lanceolate; *lower pinnae* mostly 30–45 × 10–18, elliptic, lanceolate or narrowly triangular; *pinnules* arranged catadromically, subequilateral at base, subsessile, narrowly oblong, generally 10–15 free pairs, 5–8(11) × 1.5–2.0(3.0) cm, the apex slightly falcate; *tertiary segments* 5–12(15) × 2–4(6) mm, arranged catadromically, oblong, the apex rounded to truncate, the margins entire; *axes* pubescent abaxially, the hairs either tawny or reddish, 0.5–1.2 mm long, multicellular, lax, or with the hairs shorter, stiffer, 0.1–0.3 mm long, costal scales present, inconspicuous, often at the junctures with the costules, ovate to orbicular, flaccid, brown; *grooves* pubescent within, especially at the junctures, truncated by the ridges of the next lower order. *Fertile leaves* 4-pinnate, coenosoric, or subbotryoid, if the sori discrete, then not on long stalks; *costa* pubescent, with or without ovate, denticulate scales; *sporangial stalks* paraphysate; *spores* (50)55–67(70) microns long.

Other illustrations: See Lellinger's original description (cited above) which contains a photograph of a portion of the holotype.

This plant occurs in mid-elevation forests from 750 to 2250 m in the western Andes of Colombia (Map 10). See comments under *Polybotrya alfredii* and *P. pittieri* for comparisons with those species. Considerable morphological variation exists in the specimens cited below, but I found

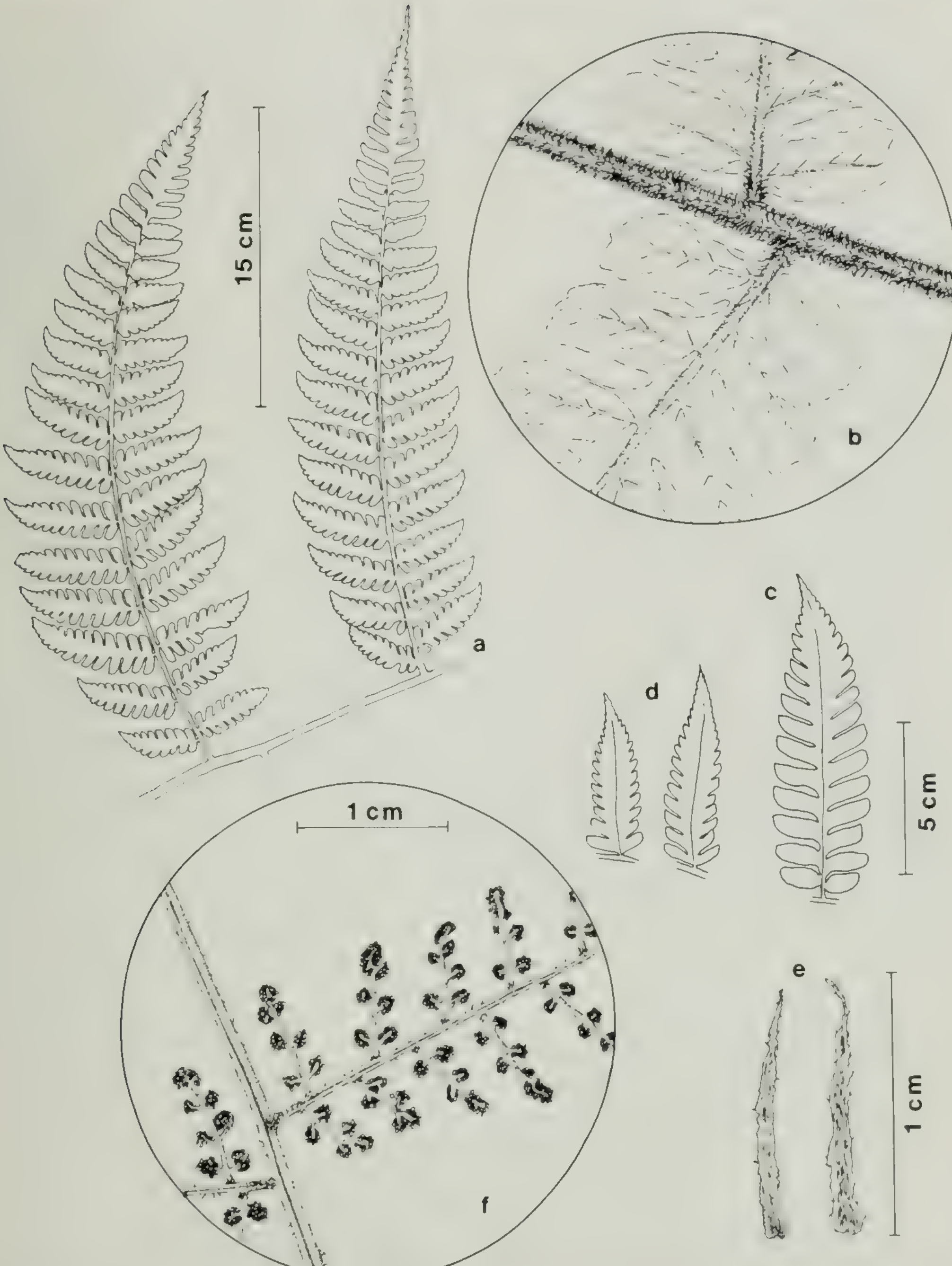

FIGURE 37. *Polybotrya lourteigiana* Lellinger. a. basal pinnae; b. pinnule bases, apex to the left; c,d. sterile pinnules, apex to the left; e. stem scales; f. fertile pinnules. a,b,c,e,f: *Lellinger & de la Sota 251* (US). d: *Cuatrecasas 15527* (US).

no constant characters to separate the extreme forms. Pubescence varies tremendously; the Lellinger and de la Sota specimens are mostly long pilose on the axes whereas the Cuatrecasas specimens have shorter, stiffer hairs. Intermediates exist, and no other characters correlate with pubescence.

The type collection consists of six sheets, of which US #2748016 is here excluded; it actually represents *P. stolzei*.

Specimens examined: COLOMBIA. **Chocó:** Trail along ridge from the confluence of the forks of the Río Mutatá above the Río Dos Bocas to the top of Alto del Buey, ca. 1450–1750 m, *Lellinger & de la Sota 251* (COL, LP, US); principal ridge and slopes 2 km E of San José del Palmar, *Lellinger & de la Sota 768a* (COL, LP, US); 0.3 km E of the Ciudad Bolívar–Quibdó road across the suspension bridge at ca. km 141, *Lellinger & de la Sota 899* (COL, LP, US); Mojarras de Tadó, 8.5 km E of Istmina, *Lellinger & de la Sota 387* (CR, COL, LP, US). **Chocó-Antioquia:** principal ridge W of La Mansa, at ca. km 105.5 of the Ciudad Bolívar–Quibdó road, *Lellinger & de la Sota 948* (COL, LP, US). **Chocó–El Valle:** Serranía de Los Paraguas, along the trail from El Cairo to Río Blanco, ca. 8 km SW of El Cairo, *Lellinger & de la Sota 843* (COL, LP, US). **El Valle del Cauca:** Hoya del Río Cali, La Margarita, *Duque-Jaramillo 1868* (COL); Cordillera Occidental, vertiente occidental, del Río Sanquinini, La Laguna, *Cuatrecasas 15527* (US); Cordillera Occidental, vertiente occidental, monte La Guarida, filo de la cordillera sobre La Carbonera, entre Las Brisas y Albán, *Cuatrecasas 22143* (F, US). **Nariño:** Municip. de Altaquer, Carretera entre Altaquer y Junín, Guyambe, *Mora 4160* (COL).

19. Polybotrya pittieri Lellinger (Fig. 38, Map 11).

Polybotrya pittieri Lellinger, Proc. Biol. Soc. Washington 89:725, fig. 6. 1977. TYPE: Colombia. Cauca: Dagua Valley, Córdoba, Pacific Coastal Zone, 30–100 m, *Pittier 587* (holotype: US!).

Stem 1 cm thick, hemiepiphytic; *scales* 9–14 × 1.0–1.4 mm, spreading, reddish, membranaceous, the margin denticulate. *Sterile leaves* up to 1.3 m long; *petiole* to 38 cm long; *lamina* triangular at base, to 60 × 90 cm, 3-pinnate at the base, 2-pinnate-pinnatifid medially, nearly glabrous on both surfaces, the apex long-tapered; *pinnules* arranged catadromically, up to 5 × 2 cm, relatively short and stubby, the base subequilateral, the apex obtuse or slightly acute; *tertiary segments* up to 1.0 × 0.5 cm, oblong; *axes* pubescent on the abaxial surface, the hairs short, stiff, ca. 0.2 mm long; *grooves* truncated by the ridges of the next lower order or only indistinctly admitted to the groove, pubescent within, the hairs reddish or tawny, 0.2–0.5 mm long. *Fertile leaves* subtriangular, 4-pinnate, botryoid, the apex long-attenuate; *pinnules* to 2.1 × 1 cm; *sori* stipitate, round, the stalks 1–4 mm long, arranged pinnately; *sporangial stalks* paraphysate; *spores* (62)65–70(77) microns long.

Other illustrations: Lellinger's original description has a photograph of the type.

Polybotrya pittieri, known from only two collections, is endemic to the western Andes of Colombia (Map 11). This species occurs at low elevations, from 30–100 m, unlike its most closely related species, *P. attenuata* and *P. botryoides*, which occur at higher elevations. It is named after Henry F. Pittier (1857–1950), a Swiss botanist and civil engineer who collected prolifically in the American tropics.

Polybotrya pittieri looks most like *P. lourteigiana*. Lellinger (1977) observed only that *P. pittieri* had a rather stiffly pilose indument on the rhachis and costae, whereas *P. lourteigiana* had a lax, hirtous indument. From the greater number of specimens of *P. lourteigiana* available to me, however, pubescence type does not appear constant. Nevertheless, *P. pittieri* seems to be a distinct species, and the best way to distinguish it is by its botryoid fertile leaves with prominently stipitate sori (Fig. 38b). *P. lourteigiana*, on the other hand, has coenosoric fertile leaves and subsessile sori (Fig. 37f). Another difference, although one that may prove inconsistent when more specimens are known, is the broadly deltate lamina of *P. pittieri*; *P. lourteigiana* is slightly reduced at the base. Using these characters, I find that the paratypes of *P. pittieri* actually belong to *P. lourteigiana*.

Polybotrya pittieri might also be confused with *P. canaliculata* since both have botryoid fertile leaves, but *P. pittieri* differs by its broadly deltate lamina, pinnule cutting, and pubescent axes that lack scales. Its spores are extremely large compared to others in the genus, suggesting that *P. pittieri* is a polyploid.

Specimens examined: COLOMBIA. **Cauca:** Dagua Valley, Córdoba, Pacific Coastal Zone, 30–100 m, *Pittier 587* (US); El Tambo, *von Sneidern 1590* (US)

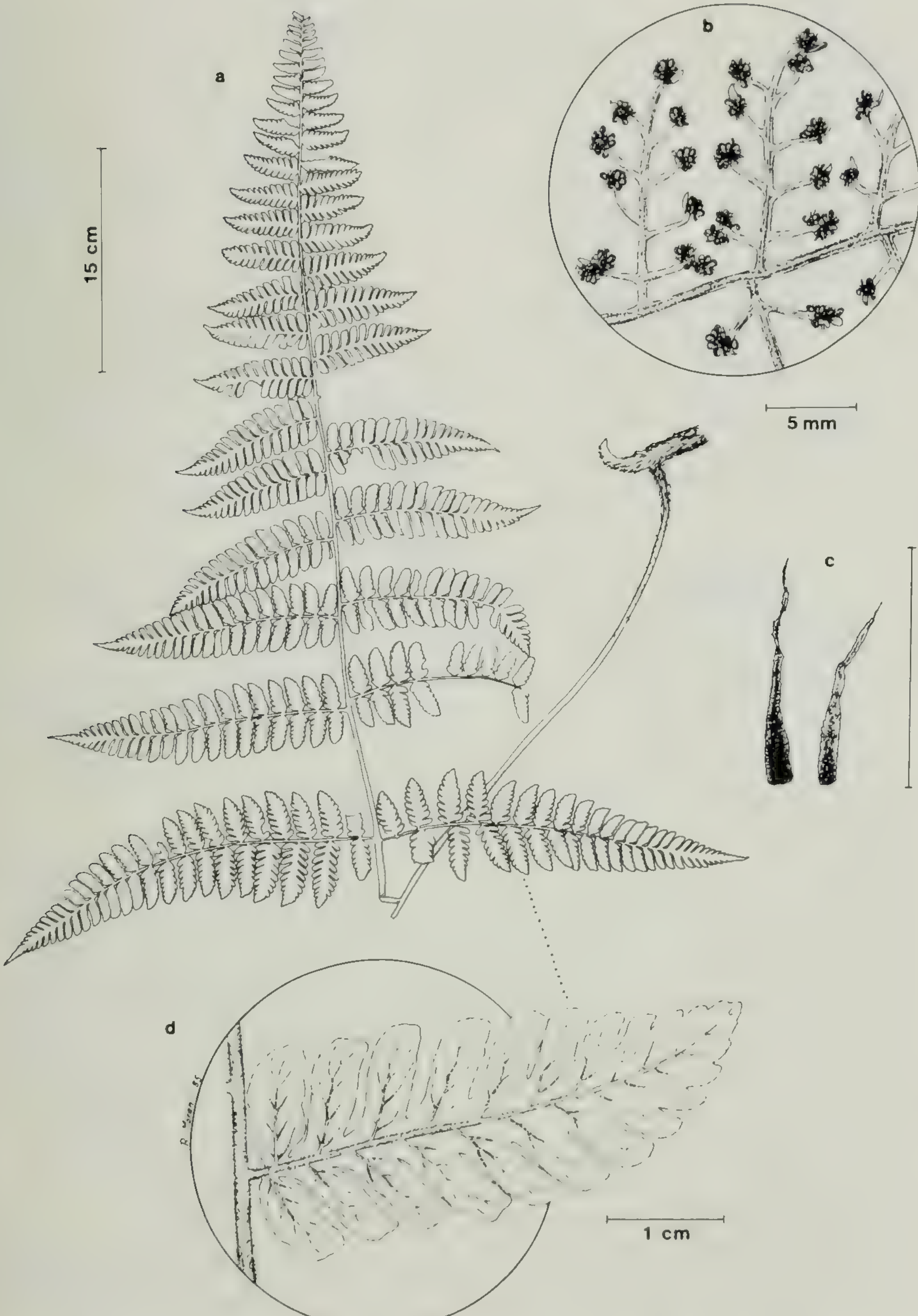

FIGURE 38. *Polybotrya pittieri* Lellinger. a. sterile leaf; b. fertile leaf; c. stem scales; d. sterile basiscopic pinnule from basal pinna. a–d: *Pittier 587* (US).

20. Polybotrya cylindrica Kaulfuss (Fig. 39, Map 16).

Polybotrya cylindrica Kaulfuss, Enum. Filicum 56. 1824. TYPE: Brazil. Santa Catarina: Island of St. Catharina, *Chamisso s.n.* (LE).

Polybotrya incisa Link, Hort. Berol. 2:135. 1833. TYPE: Brazil. No collector or date given (holotype: B!).

Acrostichum incisum (Link) Hooker, Species Filicum 5:245. 1864.

Acrostichum cylindricum (Kaulfuss) Hooker, Species Filicum 5:246. 1864.

Polybotrya frondosa Fée, Crypt. Vasc. Brésil. 1:15. 1869. TYPE: Brazil. No exact locality given, *Glaziou 2428* (holotype: K; photo GH!).

Polybotrya osmundacea var. *cylindrica* (Kaulfuss) Luetzelb. Estudo Bot. Nordeste Brazil 3:245. 1923.

Polybotrya osmundacea var. *frondosa* (Fée) Luetzelb. Estudo Bot. Nordeste Brazil 3:245. 1923.

Polybotrya osmundacea var. *incisa* (Link) Luetzelb. Estudo Bot. Nordeste Brazil 3:245. 1923.

Stem 1–2 cm thick, hemiepiphytic; *scales* dull brown, opaque, concolorous or with a very narrow hyaline border, entire, generally 6–12 mm long, the base thickened, curved, appressed. *Sterile leaves* up to 1.7 m long; *petiole* 30–50 cm long; *lamina* to 1.3 m long, 3-pinnate-pinnatifid, glabrous or pubescent with small, unicellular, whitish hairs, the margins sparsely to moderately ciliate by jointed hairs, these ca. 0.1 mm long; *pinnae* narrowly lanceolate to subdeltate, the lowermost to 52 × 28 cm; *pinnules* generally 9–14 × 3.5 × 5.5 cm, anadromic proximally, becoming catadromic distally, the acroscopic side slightly prolonged, proximal ones with a short 3–5 mm stalk; *tertiary segments* ca. 7–11 per pinnule, ovate to oblong, the largest usually pinnatisect, the apex acute or rounded; *vein tips* slightly clavate and prominulous; *axes* abaxially sparsely to densely pubescent, the hairs colorless, clear, stiff, subulate ca. 0.1–0.3 mm long, with the cross walls not easily visible, mixed with appressed, linear, scraggly, inconspicuous scales; *grooves* filled with reddish hairs. *Fertile leaves* to 90 × 62 cm, 3-4-pinnate; *ultimate segments* often oblong and appearing cylindrical due to folding back of the segment margins; *sporangial stalks* paraphysate; *spores* (55)60–66(70) microns long.

Other illustrations: Fée, Mém. Fam. Foug. 2 (Hist. Acrost.), tab. 36. 1846; *op. cit.* tab. 35 (as *P. incisa*); Brade, Bradea, 1(9):66, figs. 1 & 2; 67, figs. 16 & 17. 1969; Sehnem, Flora Ilustrada Catarinense, plate 19; plate 20 (as *P. cylindrica* var. *frondosa*). 1979.

Polybotrya cylindrica, endemic to the coastal mountains of southeastern Brazil (Map 16), is the largest and most finely divided species of *Polybotrya* in Brazil. It occurrs in wet, shaded, primary forests from 0 to 775 m. This species differs further from other *Polybotrya* species in southeastern Brazil by its stem scales that are dull brown with entire margins and the thickened and curved bases. The curved scale base orients the rest of the scale parallel to the surface of the stem, so that the scales are appressed (Fig. 39f,g). Another helpful feature in identification is the laminar margin, which is sparsely ciliate by jointed hairs less than 0.1 mm long.

Brade (1971) distinguished *P. frondosa* from *P. cylindrica* by the amount of lamina dissection. But lamina dissection exhibits complete intergradation from 2-pinnate to 3-pinnate-pinnatifid and no other characterisitcs correlate with it (Fig. 39a-d).

Although I have not seen the type of this species, the original description by Kaulfuss is sufficient to ascertain his plant's identity. He specifically mentions the ciliate margins that distinguish this plant from others in southeastern Brazil. Furthermore, this species is the only *Polybotrya* that grows on the Island of Santa Catarina, where the type was collected. The specific epithet probably refers to the fertile segments which, upon drying, reflex so that the sori appear on all surfaces, thereby imparting a cylindrical shape to the segments.

Specimens examined: BRAZIL. **Espírito Santo:** Municipio de Cachoeira de Itapemirim–Vargem (?), *Brade 19972* (HB, MO, NY). **Paraná:** Mun. Guaratuba, Pedra Branca de Araraquara, *Hatschbach 8141* (US); Pedra Branca de Araraquara, *Hatschbach 7424* (US); no locality, *Hatschbach 10749* (NY); no locality, *Dusén 13658* (GH); Porto Dom Pedro II, *Dusén 4423*(BM);

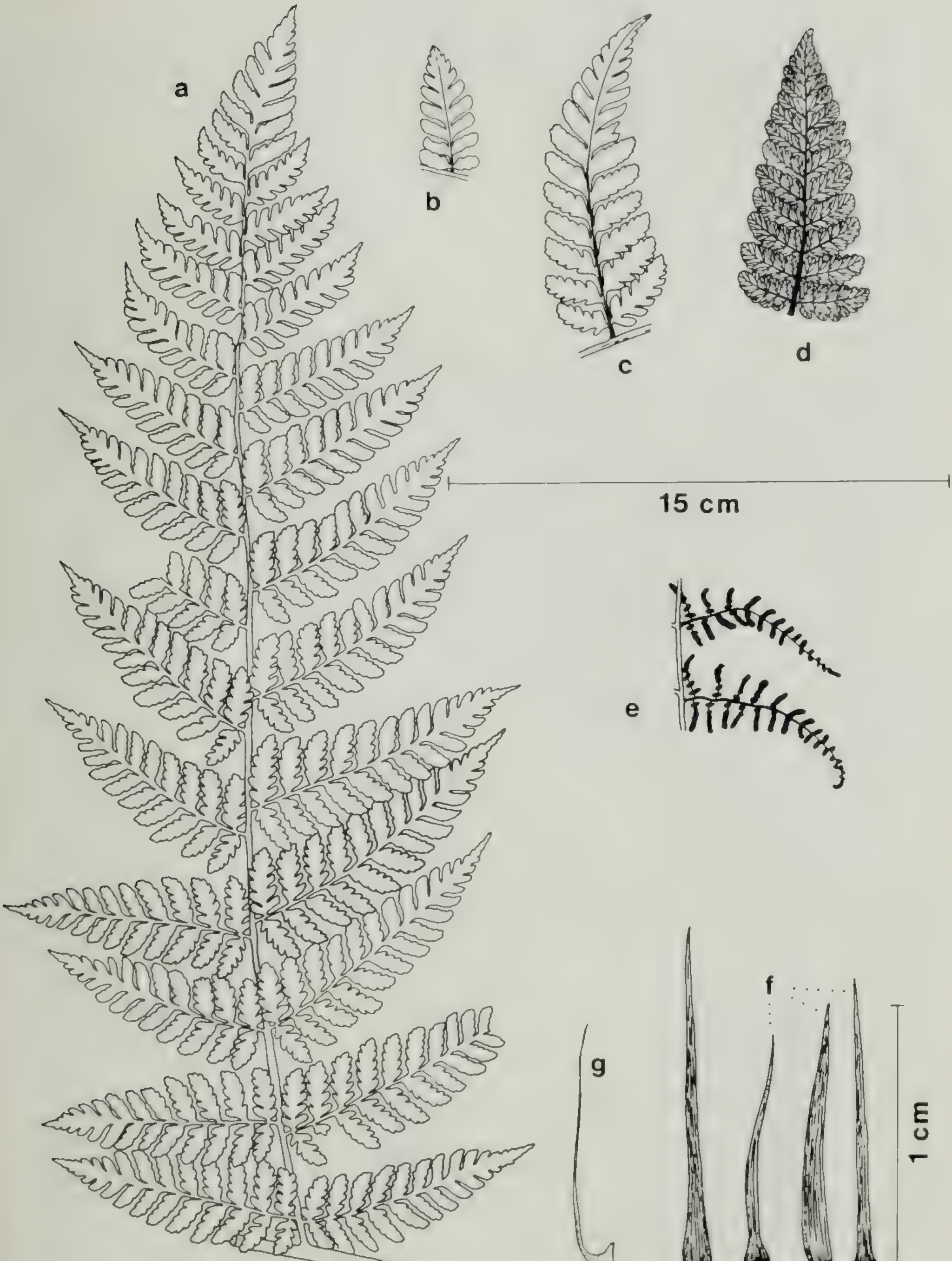

FIGURE 39. *Polybotrya cylindrica* Kaulfuss. a. sterile pinna; b–d. sterile pinnules showing variation in amount of dissection; e. fertile pinnules; f. stem scales, top view; g. stem scale, side view. a,e: *Goedas 217* (NY). b: *Mosen 3050* (B). c,f,g: *Schmalz 158* (UC). d: *Dusén 6926* (F).

Volta Grande, *Dusén 6984* (BM); Porto de Cima, *Dusén 6926* (F, GH, LIL, MO, NY, PH, UC, Z); Tacarehy, *Dusén 15351* (BM, F, PH), *15353* (GH, MO, PH, UC, Z). **Rio de Janeiro:** without locality, *Hunnewell 18511* (MICH); Distrito Federal, Guanabara, Represa Camori, *Brade 12576* (RB); Rezende, 80 mi WNW of Rio, on Paraiba River, Rio Palmital, *Castellanos 25710* (F); Serra de Itatiaia, *Brade 12614* (NY, RB); Brene, *Glaziou 955*(RB); vicinity of Meio da Serra, *Smith & Brade 2286* (GH); Estrada Velha de Barrira a Teresópolis, *Duarte & Pereira 65323* (F, LP); Corcovado, *Miers s.n.* (NY); Teresópolis, *Brade 9365* (NY, UC); Serra da Carioca, *Brade 13982* (RB). **Rio Grande do Sul:** S. Leopoldo, *Lehnun 2562* (LIL); Porto Alegre, *Fargens 251* (UC). **Santa Catarina:** Municip. Ibirama, Horto Florestal, *Smith & Klein 7546* (US); Horto Florestal, I.N.P., Ibirama, *Reitz & Klein 1101* (US), *1102* (US), *2665* (US), *3466* (US); Blumenau, Warnow, *Goedas 217* (NY, UC, US); Itajaí, *Reitz 151* (LIL); Municipality Brusque, Azambruja, *Smith and Reitz 6135* (COL, GH, MO, US); Reserva Florestal, dos Piloes, *Duarte 3179* (LP, NY); Mina Velha, Garuva, São Francisco do Sul, *Reitz & Klein 4635* (US), *4682* (US); Sabia, Vidal Ramos, *Reitz & Klein 5108* (US); Passo Mansa, *Haerchen 124* (NY); Joinville, *Schmalz 78* (MO), *158* (NY, UC); Tres Barras, Garuva, São Francisco do Sul, *Reitz & Klein 5549* (US); Sta. Catherine 1834, *Gaudichaud 73* (P); Azambuja–Brusgui, *Reitz 2825* (LIL, P); Blumenau, *Muller 6039* (MICH). **São Paulo:** São Bento, *Luetzelburg 254* (MICH, US); Serra da Bocaina, *Brade 20931* (LP); Morro das Pedras, Iguape, *Brade s.n.* (US); Paranapicaba, Biological Station, *Handro 1229* (GH, US); Agua funda, *Handro 2228* (GH, US); Serra do Mar, *Wacket 21556* (GH); Campo Grande to Alto da Serra, 40 km SE of São Paulo, *Tryon & Tryon 6591* (GH); Santos, 1874, *Mosen 3050* (B, P). **State unknown:** *Glaziou 2428* (photo of K specimen at GH); no locality, *Claussen s.n.* (P); *Micken s.n.* (NY); Capão do Fradie, *Schneus 3412* (GH); Morro do Antão, *Sehnem 3092* (GH).

21. Polybotrya hickeyi Moran, *sp. nov.* (Fig. 40, Map 13).

Polybotrya hickeyi Moran, *sp. nov.* TYPE: Bolivia. Cochabamba: Prov. Chapare, road from Cochabamba to Villa Tunari, in thick rain forest, very heavily shaded, on trunk of *Ficus* 1700 m, 23 March 1980, *Hickey 801* (with Eshbaugh) (holotype: GH!; isotype: MU).

Caulis hemiepiphyticus, 1–2 cm diam.; squamae atrobrunneae, vulgo opacae, leviter nitidae, concolores vel marginibus tenuioribus et pallidioribus ad apicem; lamina usque ad 3-pinnata-pinnatifida, deltata, usque ad 1 m longa, leviter pubens inferne, pilis cylindricis, appressis, usque ad 0.1 mm longis; pinnae usque ad 46 × 25 cm, deltatae, paribus proximalibus acroscopice prolongatis; pinnulae catadromicae supra basin, deltatae, oblongae vel lanceolatae; costae sine sulcis prominentibus; venae prominulae superne, apice leviter incrassatae. Sori discreti, rotundi, oppositi vel subopposití.

Stem 1–2 cm thick, hemiepiphytic; *scales* dark chocolate brown, mostly opaque, concolorous, or the apex with thinner, lighter borders, the margins denticulate to entire, the base thickened, attached across its full width. *Sterile leaves* up to 1.5 m (?); *petiole* with thin, ovate to lanceolate scales; *lamina* to 3-pinnate-pinnatifid, deltate, to about 1 m long, the abaxial surface slightly puberulent, the hairs cylindrical, appressed, up to 0.1 mm long; *pinnae* up to 46 × 25 cm, deltate, the proximal pair basiscopically prolonged, the distal ones gradually becoming acroscopically prolonged; *pinnules* catadromic above the base, deltate to oblong-lanceolate, the basiscopic margins thickened and decurrent on the costa, the base slightly prolonged acroscopically, the apices acuminate; *tertiary segments* also with a thickened, decurrent, light-colored basiscopic margin; *veins* prominulous adaxially, the tips thickened and ending just behind the margin; *costules* bordered by a raised, erect flap or wing of tissue; *axes* often not prominently grooved, pubescent by ca. 0.1 mm long, colorless, erect hairs, the scales appressed, denticulate, flexuose. *Fertile leaves* botryoid; *sori* with few fusions, arranged mostly oppositely or suboppositely.

Polybotrya hickeyi grows in high elevation forests in the Andes of Colombia and Bolivia; it has not yet been collected from Ecuador or Peru (Map 13). This species looks most like *P. puberulenta*—see that species for comparison. This plant is named for one of the collectors, Dr. R. James Hickey, who has made important contributions to the study of *Isoetes* and *Lycopodium*.

The Colombian specimens look like the Bolivian type specimen except for the stem scales. The Bolivian type has dark, chocolate brown scales with denticulate margins and lighter borders apically (Fig. 40g). The Colombian specimens have merely dull brown, concolorous scales with

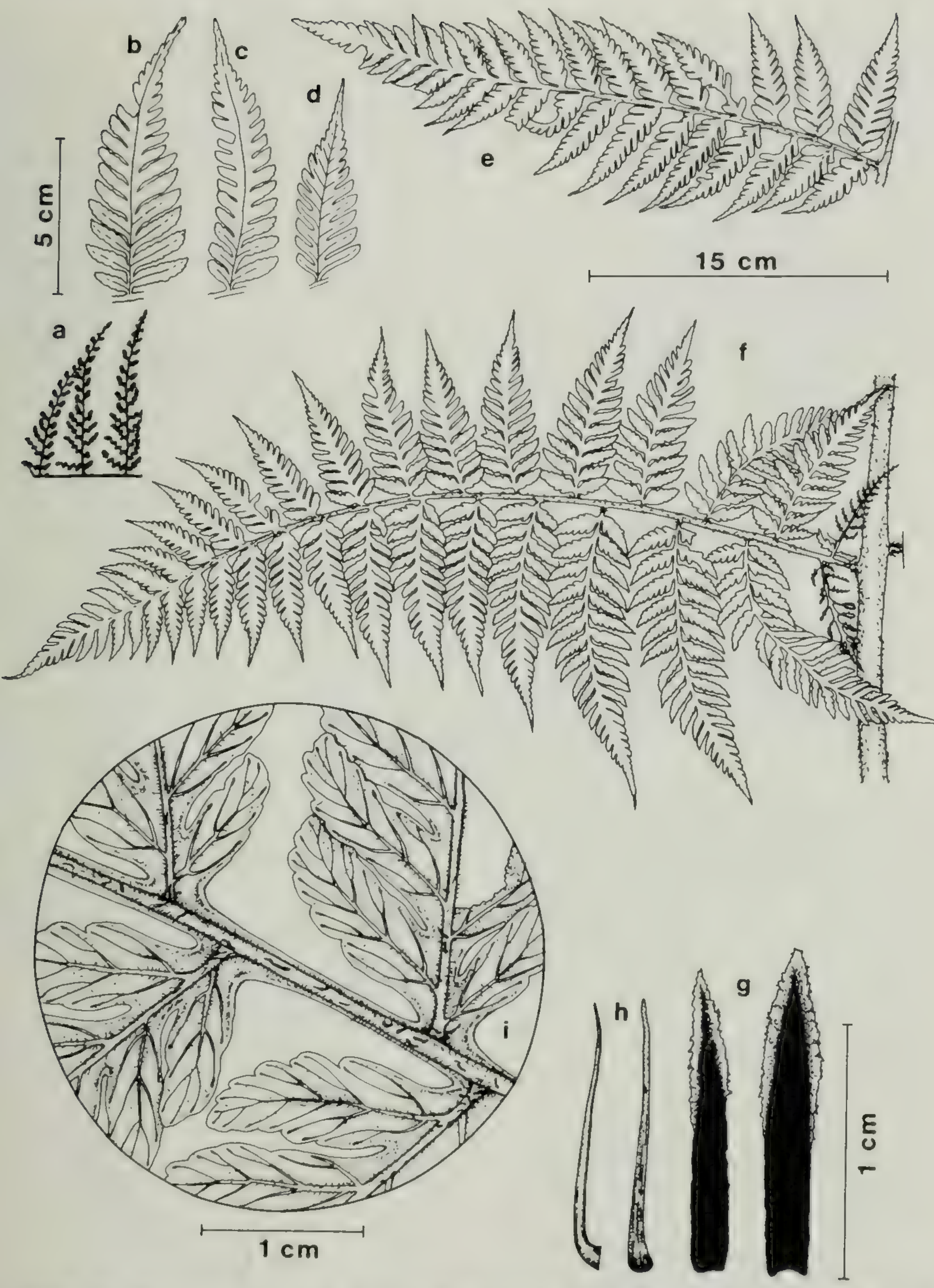

FIGURE 40. *Polybotrya hickeyi* Moran. a. fertile pinnules; b,c,d. sterile pinnules, acroscopic side to the right; e. medial pinna; f. basal pinna (note that the two proximal basal pinnules are fertile); g. stem scales (Bolivia); h. stem scale (Colombia); i. abaxial surface of distal pinnules. a,d: *Ludwig 262* (NY). b,h: *Grant 10283* (F). c: *Killip & Smith 20210* (US). e,f,g,i: holotype, *Hickey 801*, with Eshbaugh (GH).

entire margins and a prominently curved and thickened base; therefore, they appear appressed (Fig. 40h). This thickened and curved scale base appears somewhat elevated, like those of *P. caudata* and *P. cylindrica* . The lamina of *P. hickeyi* turns a peculiar yellowish green upon drying.

Specimens examined: COLOMBIA. **Cauca:** W slope of W Cordillera, above Carpinteria, *Alston 8278* (BM). **Cundinamarca:** Cordillera Oriental, Toquiza, Gazaunta Valley, Cordillera de Helicona, 15 km NW of Medina, 2200 m, *Grant 10283* (F, US); Fusagasugá, *Ludwig 262* (BM, MO, NY). **Norte de Santander:** Pica-Pica Valley, above Tapata (N of Toledo) 2100–2400 m, *Killip & Smith 20210* (GH, NY, US).

Bolivia. **Cochabamba:** Prov. Chapare, road from Cochabamba to Villa Tunari, 1700 m, *Hickey 801* with Eshbaugh (GH).

22. Polybotrya puberulenta Moran, *sp. nov.* (Fig. 41, Map 13).

Polybotrya puberulenta Moran, *sp. nov.* TYPE: Ecuador. Napo: camino Baeza–Tena, 5 km al sur de Cosanga. Cordillera Oriental, bosque perturbado, 1100 m, 4 de enero 1984, *Moran 3528* (holotype: F!; isotypes: COL!, GH!, LPB!, MO!, NY!, Q!, QCA!, UC!, US!, VEN!).

Caulis hemiepiphyticus; squamae aurantiacae sordidae vel luteae, membranaeae, late patentes, centro leviter fuscatae, marginibus denticulatis vel erosis; lamina 2-pinnata-pinnatisecta perlate ovata, crassa, flavovirentes pallide, pubents utrinque, pilis patentibus, flexuosis, ca. 0.1 mm longis; pinnae usque ad 34 × 18 cm, infimus basiscopice prolongatae; pinnulae catadromicae oblongae, in margine incrassatae et decurrentes; lobi tantum crenati, apice truncati vel rotundati; venae prominulae superne, apice leviter incrassatae. Folia fertilia 4-pinnata, axibus dense pubescentibus, pilis 3–5 mm longis et squamis linearibus, appressis vel leviter patentibus; segmenta opposita vel subopposita, receptaculo pubescenti, pilis 1–2 mm longis, articulatis.

Stems 1–2 cm thick, hemiepiphytic; *scales* yellow to sordid orange, darker in the center with light yellow borders, membranous, spreading, 1–3 mm wide, the margins erose to denticulate, attached across the width of the narrowed base, in fresh material somewhat rugose transversely. *Sterile leaves* up to 1.2 m long; *petiole* up to 27 cm long; *lamina* to 2-pinnate-pinnatisect, broadly ovate, thick and somewhat fleshy in living material, color light yellowish green, puberulent on both surfaces, the hairs spreading, flexuous, ca. 0.1 mm long, intergrading with the scales on the lower surface; *pinnae* up to 34 × 18 cm, the proximal pairs basiscopically prolonged, the distal ones gradually becoming equilateral or slightly acroscopically prolonged; *pinnules* catadromic throughout, oblong, the basiscopic margin thickened, decurrent on the costa, the apices obtuse to acute, base cuneate and slightly prolonged acroscopically; *costules* bordered by a raised flap of lighter colored tissue; *lobes* of the largest pinnules merely crenate, the margins thickened, the apices obtuse or truncate; *veins* prominulous adaxially, the tips slightly thickened and ending just behind the margin; *axes* evenly pubescent abaxially, the hairs 0.1 mm long, tawny, erect, scales caducous, usually lacking; *grooves* pubescent within, becoming shallow and flat at the junctures, not admitted to the groove of the next lower order. *Fertile leaves* 4-pinnate, the axes densely pubescent, the hairs jointed, 3–5 mm long, the scales 5–10 mm long, linear, appressed to slightly spreading; *sori* opposite or subopposite; *sporangial stalks* paraphysate; *receptacle* pubescent by jointed hairs, 1–2 mm long, that protrude beyond the sporangia; *spore size* unknown.

Polybotrya puberulenta grows at high elevations in the Andes of Ecuador, Bolivia, and probably Peru (Map 13). The specific epithet refers to the sterile lamina, which is puberulent on both surfaces. Another distinctive feature of this species is the stem scales, which are relatively wide (1–3 mm), thin, spreading and yellowish when viewed with transmitted light. The lamina is relatively thick and fleshy; the mesophyll cells apparently collapse when dry and the veins become prominulous. The lamina, which is always broadest at the base, has a peculiar light greyish green color when dry.

This species differs from *P. hickeyi* in several characteristics of the stem scales, pinnule arrangement, lamina dissection, pubescence, paraphysis length, and scalyness of the major axes. Both species, however, have thickened, decurrent, basiscopic margins. The medial, less cut pinnules of *P. hickeyi* may approach in outline those of *P. puberulenta*, but the largest pinnules of the basal

FIGURE 41. *Polybotrya puberulenta* Moran. a. pinnules; b. stem scales; c. sterile leaf; d. abaxial surface of costa and pinnules. a–d: *Moran 3528* (F).

pinnae are much more highly divided in *P. hickeyi* (compare Figs. 40f and 41a).

Unfortunately, Rusby's Bolivian collection consists only of the fertile leaf, but I believe it belongs to this species because of its cutting, indument type, and yellowish stem scales. The long, protruding paraphyses are easily seen with a hand lens and offer an excellent character to distinguish this species from *P. hickeyi*.

Specimens examined: ECUADOR. **Napo:** camino Baeza–Tena, 5 km al sur de Cosanga, Cordillera Oriental, bosque perturbado, 1100 m, *Moran 3528* (COL, F, GH, LPB, MO, NY, Q, QCA, UC, US, VEN).

BOLIVIA. **La Paz:** Yungas, 6000 ft, "only the fertile frond collected," *Rusby 443* (NY).

23. Polybotrya alata Moran, *sp. nov.* (Fig. 42, Map 14).

Polybotrya alata Moran, *sp. nov.*, TYPE: Panama. Panamá: Campo Tres, 3 mi NE of Altos de Pacora, primary forest, alt 500–800 m, epiphytic, the caudex closely appressed, sterile, 10 March 1973, *Croat 22706* (holotype: MO!; isotype: L!).

Caulis hemiepiphyticus usque ad 2.5 cm diam.; squamae lineares, 15–25 × 0.8–1.2 mm, chrysobrunneae, concolores vel centris leviter fuscatis, appressis, ascendentibus, marginibus denticulatis. Lamina 2-pinnata-pinnatifida, superne glabra, inferne pubens, pilis circa 0.1 mm longis, niveis, subulatis; pinnae usque ad 30 × 8 cm, anguste triangulares, apicibus attenuatis, zonis mediis alatis secus costam; pinnulae catadromicae, usque ad 6 × 2 cm, lobis catadromicis, crenatis; rhachis et costae pubescentes et squamatae. Folia fertilia ignota.

Stem 2.5 cm thick, hemiepiphytic; *scales* linear, 15–25 × 0.8–1.2 mm, membranaceous, golden brown, concolorous or with a slightly darkened central stripe, appressed-ascending, margins denticulate. *Sterile leaves* up to 1.3 m long; *petiole* to 45 cm long, scaly, pubescent with 0.2 mm long, unicellular, colorless hairs; *lamina* 2-pinnate-pinnatifid, the adaxial surface glabrous, the abaxial surface lightly to moderately pubescent, the hairs unicellular, less than 0.1 mm long, whitish, subulate; *pinnae* up to 30 × 8 cm, narrowly triangular with a long tapering apex, 3–4 times as long as broad, the lowest becoming pinnatifid in the apical one-third, the transition zone between pinnate and pinnatifid marked by a narrow, straight, decurrent, green wing parallel to the costa; *pinnules* catadromically arranged in the medial pinnae, lobed almost to the costule, inequilateral at base, up to 6 × 2 cm, the proximal acroscopic ones longer than the proximal basiscopic; *pinnule lobes* catadromically arranged, the margins crenate, the apices rounded; *axes* pubescent abaxially, the hairs 0.1–0.2 mm long, subulate, colorless, often difficult to see on the lamina, intermixed on the costae with long, scraggly, subclathrate, denticulate scales; *groove* usually glabrous, abruptly truncated by the raised ridge of the costal groove, the junctures short-pubescent. *Fertile leaves* unknown.

Polybotrya alata has been collected only twice, both times in the mountains of Panama (Map 14), but I suspect it also occurs in the mountains of southern Costa Rica. Distinctive features of this species are the narrowly triangular pinnae with long attenuate apices and the pinnules that are lobed almost to the costule, thereby making the lamina 2-pinnate-pinnatifid (Fig. 42a). The transition zone from the free pinnules to the pinnatifid apex differs from all other species of *Polybotrya* by the thin, basally decurrent, green wing, which imparts an alate appearance to the costa (Fig. 42c). The stem scales are also distinctive by their long length (15–25 × 0.8–1.2 mm) and shiny, golden brown color.

The short, even pubescence on the abaxial surface of the leaf separates *P. alata* from all other Central American *Polybotrya*, except *P. caudata*, which can also have pubescent leaves. The laminar hairs of *P. caudata*, however, are longer (1–3mm) than those of *P. alata* and are 4–10 celled. The two species also differ sharply by their stem scales. The only other Central American species with which *P. alata* could be confused is *P. osmundacea*, but that species is easily distinguished by its anadromic pinnule arrangement and nonalate costae. Furthermore, the costular groove of *P. alata* is truncated by the ridges of the costa; in contrast, *P. osmundacea* has uninterrupted, decurrent grooves (Fig. 47h).

Specimens examined: PANAMA. **Panamá:** Campo Tres, 3 mi NE of Altos de Pacora, *Croat 22706* (MO, L). **Veraguas:** 5 mi W of Santa Fe on road past Escuela Agricola Alto Piedra on Pacific side of divide, 800–1200 m, *Croat 23011* (MO).

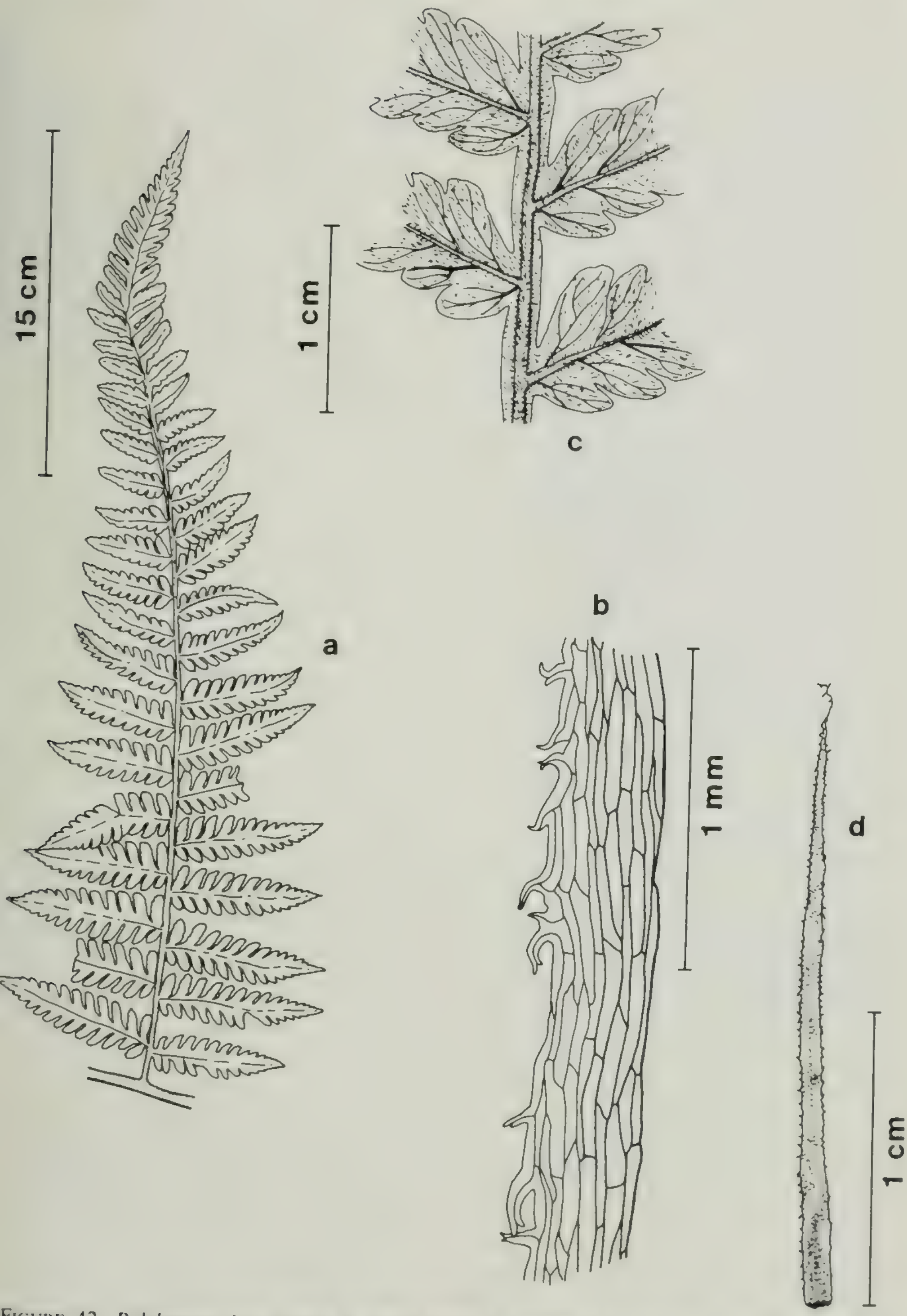

FIGURE 42. *Polybotrya alata* Moran. a. sterile pinna; b. margin of stem scale; c. abaxial surface of distal pinnules (note pubescence and decurrent pinnule bases); d. stem scale. a–d: *Croat 22706* (MO).

24. Polybotrya aequatoriana Moran, *sp. nov.* (Fig. 43, Map 15).

Polybotrya aequatoriana Moran, *sp. nov.* TYPE: Ecuador. Napo: Cordillera Oriental, camino Baeza–Tena, 34 km al sur de Baeza, 2100 m, 30 de diciembre 1983, *Moran 3512* (holotype: F!; isotypes: AAU!, COL!, GH!, LPB!, MO!, NY!, Q!, QCA!, UC!).

Caulis hemiepiphyticus, 1.5–3.4(4.0) cm diam.; squamis sordide aurantiaco-luteis, nitidis, membranaceis, implexis, lanatis, in margine minute denticulatis, 1–2(3) × 12–20(25) mm; lamina lanceolata, usque ad 1.4 × 0.7 m, 2-pinnata-pinnatifida, modice vel sparse puberula subter, pilis appressis, 0.1–0.3 m longis; pinnae longideltatae, 25–35 × 13–18(20) cm; pinnulae catadromicae, acroscopice prolongatae, basiscopice valde obliquae; lobi integri vel vade crenati; rhachis et costae pubescentes, pilis rigidis albidis, sulcis profundis pubescentibus. Pinnulae fertiles lineares, vulgo 4–6 × 0.5–1.0 cm, segmentis oppositis vel suboppositis circularibus vel oblongis, 3–5 × 1–2 mm.

Stem 1.5–3.5(4) cm thick, hemiepiphytic; *scales* dingy orange yellow, mostly darkening upon drying, shiny, membranous, tangled and woollike, the margins minutely denticulate, 1–2(3) × 12–20(25) mm. *Sterile leaves* up to 1.6 m long; *lamina* lanceolate, to 1.4 × 0.7 m, 2-pinnate-pinnatifid, moderately to lightly pubescent below, the hairs fine, appressed, 0.1–0.3 mm long, grading into scales along the axes, often with a few scattered resinous, circular glands (use at least 30 ×), the margins somewhat thickened and lighter colored, often becoming revolute upon drying; *pinnae* long-triangular, 25–35 × 13–18(20) cm; *pinnules* arranged catadromically above the base, prolonged acroscopically, reduced and very oblique basiscopically; *lobes* entire or rarely shallowly crenate; *axes* pubescent below with unevenly scattered, whitish, erect hairs 0.1–0.2 mm long, scaly by linear, flexuous, darkened, often appressed scales, these most abundant at the junctures; *grooves* deep and distinct, filled with hairs, these sometimes clavate, ca. 0.1 mm long, reddish, the ridges well defined, stramineous, continuous with those of the costules but truncated by the ridges of the rhachis. *Fertile leaves* botryoid; *pinnules* linear, mostly 4–6 × 0.5–1.0 cm; *sori* arranged oppositely or suboppositely, round to oblong; *sporangial stalks* paraphysate; *spore size* unknown.

Polybotrya aequatoriana occurs in the cloud forests of Ecuador and Bolivia (Map 15), from 2100–2410 m, the highest known altitudinal range of any species of *Polybotrya*. *Polybotrya aequatoriana* is named for Ecuador, where I collected the type.

Polybotrya aequatoriana can be easily separated from *P. hickeyi* and *P. appressa* by its stem scales, which are thin, yellowish orange, and membranaceous (Fig. 43b); see *P. appressa* for further comparison with that species. *Polybotrya aequatoriana* has highly reduced basiscopic lobes on the sterile pinnules (Fig. 43c), and the fertile pinnules are much narrower than those of other congenerics.

Specimens examined: ECUADOR. **Napo:** Cordillera Oriental, camino Baeza–Tena, 34 km al sur de Baeza, 2100 m, *Moran 3512* (AAU, COL, F, GH, LPB, MO, NY, Q, QCA, UC), *3585* (F, Q, QCA); road Baeza–Lago Agrio, ca. 114 km from Lago Agrio, 1750 m, *Øllgaard et al. 35776* (AAU, QCA).

BOLIVIA. **La Paz:** Prov. Sud Yungas, Huancane, 7.5 km hacia el sud sobre el camino nuevo, 2410 m, *Beck 3108* (LPB); same locality, but at 6.5 km, 2280 m, *Beck 3060* (LPB, NY).

25. Polybotrya appressa Moran, *sp. nov.* (Fig. 44, Map 17).

Polybotrya appressa Moran, *sp. nov.* TYPE: Ecuador. Napo: Cordillera Oriental, camino Baeza–Tena, 34 km al sur de Baeza, bosque virgen, 2100 m, 24 de enero 1984, *Moran 3586* (holotype: F!; isotypes: GH!, MO!, NY!, Q!, QCA!, US!).

Caulis hemiepiphyticus, 1–2 cm diam.; squamae concolores, obscure brunneae, integrae, appressae, vulgo 1–2 × 0.1–0.2 cm; lamina ovata vel late deltata, 2-pinnata-pinnatifida, superne glabra, inferne pilosa, pilis dispersis, ca. 0.1 mm longis; pinnae usque ad 37 × 18 cm; pinnulae prolongatae acroscopice, latis basiscopicis reductae; lobis rotundatis vel plusminusve truncatis; rhachis et costae aequaliter pubescentes, pilis usque ad 0.1 mm longis, sulcis glabris. Folia fertilia ignota.

Stem 1–2 cm thick, hemiepiphytic; *scales* concolorous, dull brown, thick, opaque, entire,

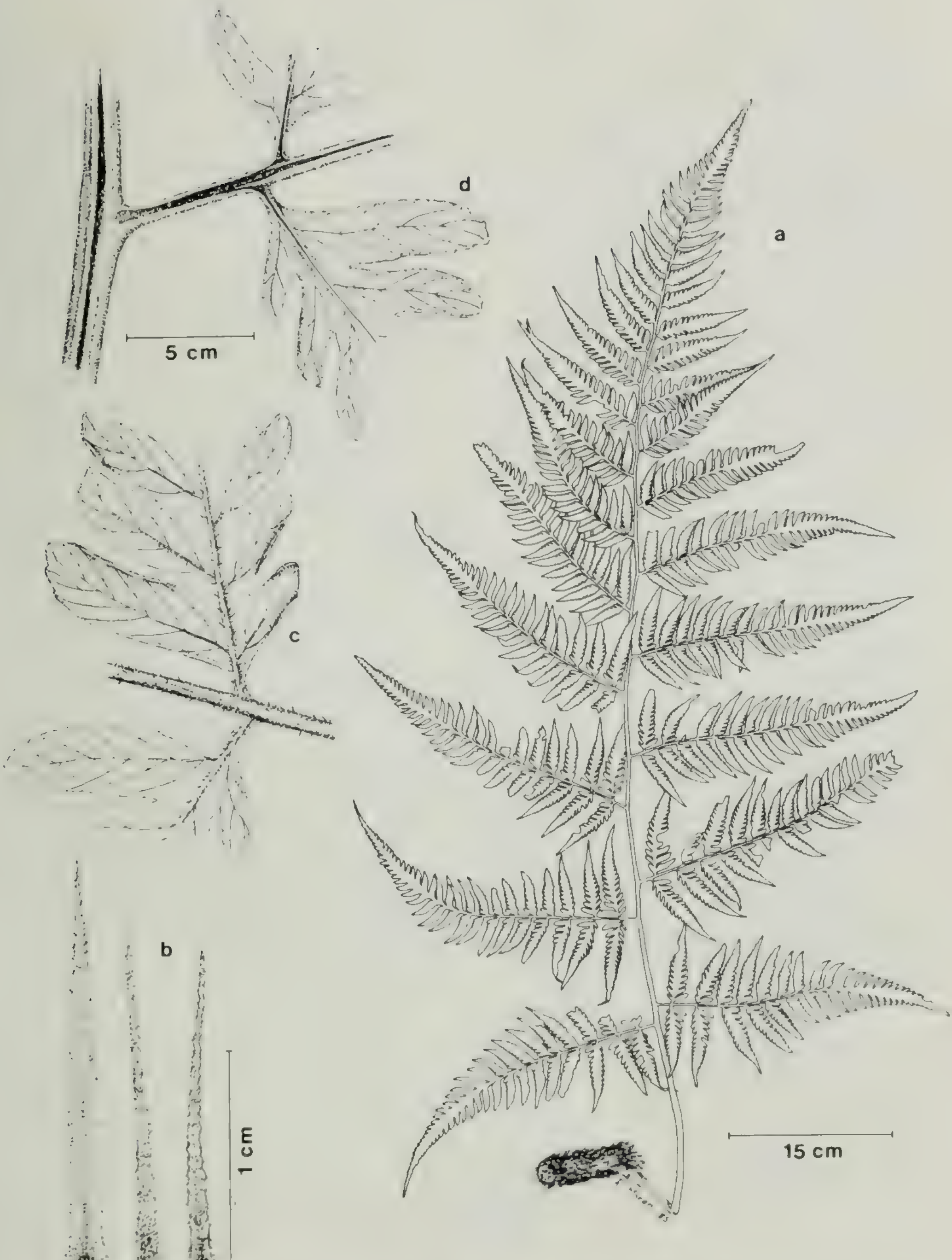

FIGURE 43. *Polybotrya aequatoriana* Moran. a. sterile leaf; b. stem scales; c. costa and pinnule bases, abaxial view (note only scattered hairs); d. rhachis, costa, pinnule bases, adaxial view, groove minutely pubescent, thin. a–d: *Moran 3512* (F).

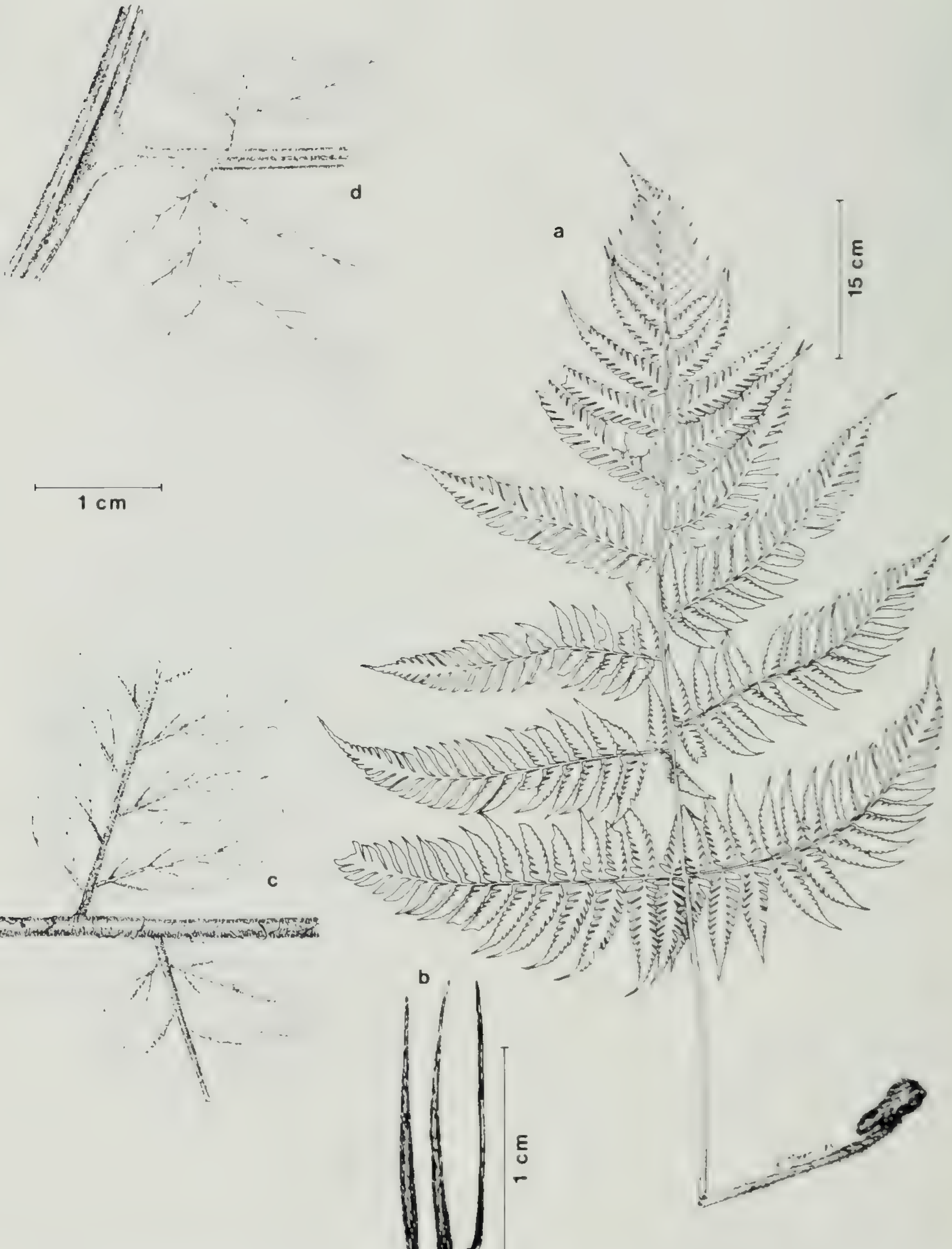

FIGURE 44. *Polybotrya appressa* Moran. a. sterile leaf; b. stem scales; c. costa and pinnule bases, abaxial view; d. costa and pinnule bases, adaxial view. a–d: *Moran 3586* (F).

appressed, mostly 1–2 × 0.1–0.2 cm. *Sterile leaves* up to 1.5 m long; *lamina* ovate to broadly deltate, dark green above, slightly paler below, 2-pinnate-pinnatifid, up to 1.3 × 0.74 m, glabrous adaxially, abaxially with a few scattered, appressed hairs, these less than 0.1 mm long, intergrading with scales on the costae; *pinnae* to 37 × 18 cm, widest at the base, the apex long-tapering, the acroscopic basal pinule usually prolonged beyond the rest; *pinnules* arranged catadromically, prolonged acroscopically and reduced basiscopically at the base, the proximal ones with acuminate apices, the distal ones with falcate and truncate apices; *lobes* rounded to somewhat squarish, entire or rarely minutely serrate at the apex; *axes* evenly pubescent abaxially, the hairs short, less than 0.1 mm long, the costal scales present or caducous and absent, linear to lanceolate, appressed, light brown, thin; *grooves* sparsely pubescent within, not very deep or prominent, bordered by broad, shallow ridges, not admitted to the groove of the next lower order. *Fertile leaf* unknown.

Polybotrya appressa is known only from the eastern Andes of Ecuador (Map 17), where it grows in cloud forests at high elevations. This new species is named for its distinctive, appressed stem scales (Fig. 44b), which help separate it from similar species, many of which have spreading, membranous stem scales. *Polybotrya caudata* has similiar dull, thick, opaque stem scales, but that species does not grow at high elevations.

Polybotrya appressa differs from *P. aequatoriana*, a closely allied Ecuadorian species, by its stem scales, groove architecture and pubescence, and lamina shape. *Polybotyra hickeyi* is also very closely related, especially by its short, even, abaxial, costal pubescence, and the indistinct adaxial grooves that are glabrous within; but it differs primarily by its more finely cut lamina. In addition, the lamina of *P. appressa* is dark green, in contrast to the pale yellowish green laminae of *P. hickeyi* and *P. aequatoriana*.

Specimens examined: ECUADOR. **Napo:** Cordillera Oriental, camino Baeza–Tena, 34 km al sur de Baeza, Bosque virgen, 2100 m, 24 de enero 1984, *Moran 3586* (F, GH, MO, NY, Q, QCA, US); Cordillera Oriental, 5 km al sur de Cosanga, camino Baeza–Tena, 1000 m, 4 de enero 1984, *Moran 3527* (Q, QCA); Cerro Huacamayos, on road Baeza–Tena, ca. 34 km from Baeza, *Øllgaard et al. 53824* (AAU, QCA).

26. Polybotrya altescandens C. Chr. (Fig. 45, Map 12).

Polybotrya altescandens C. Chr., Index Filicum 7. 1905. *nom. nov.* for *Acrostichum chrysolepis* Sodiro, *non* Fée 1869.

Acrostichum chrysolepis Sodiro, [Anal. Univ. Quito (XI)77:561. 1894.] Crypt. Vasc. Quit. 485. 1893. *nom. illeg.*, *non* Fée 1869. TYPE: Ecuador. Pichincha: selva tropical, de Pilaton-Toachi, septiembre 1892, *Sodiro s.n.* (holotype: P!).

Stem (1)2–3(4) cm thick, hemiepiphytic; *scales* golden to yellowish, mostly concolorous, shiny, tangled and forming a dense "wool" around the stem, linear, 0.6–1.3 × 15–25(32) mm, base cordate and darkened at the point of attachment. *Sterile leaves* up to 2 m long; *lamina* to 1.65 m long, lanceolate, to 2-pinnate-pinnatifid or rarely 3-pinnate, usually moderately pubescent, the hairs fine, appressed, more or less cylindrical, multicellular, 0.2–0.4 mm long, intergrading with scales on the costa; *pinnae* evenly tapering to a truncate base, the acroscopic side slightly prolonged, especially in the distal pinnae, 14–25(35) × 3–10(17) cm, soon becoming pinnatifid in the distal portions; *pinnules* anadromous or subequal proximally, catadromous distally, entire to coarsely serrate, the basal acroscopic one almost always conspicuously prolonged beyond the others; *axes* pubescent abaxially, the hairs subulate, colorless, 0.1–0.2 mm long, unicellular, the scales few, scattered, denticulate; *grooves* slightly pubescent within, those of the costule decurrent into those of the costa, costal groove gradually becoming shallow and expanded before the juncture with the rhachidial groove; *veins* in pinnate groups, in large pinnae and pinnules the lowermost basiscopic veinlet often springing directly from the costa or costule, appearing as a single isolated veinlet between the main pinnate groups. *Fertile leaves* 3-pinnate, pubescent by jointed hairs 0.5–1.0 mm long, these grading into linear, tortuous scales; *sori* obovate or oblong; *sporangial stalks* paraphysate; *spores* (54)59–69(72) microns long. $n = 41$.

This species has an altitudinal range of (800)1200–2500 m. Most of the collections come from the western cordillera of Ecuador, but two apparently disjunct locations occur in Colombia

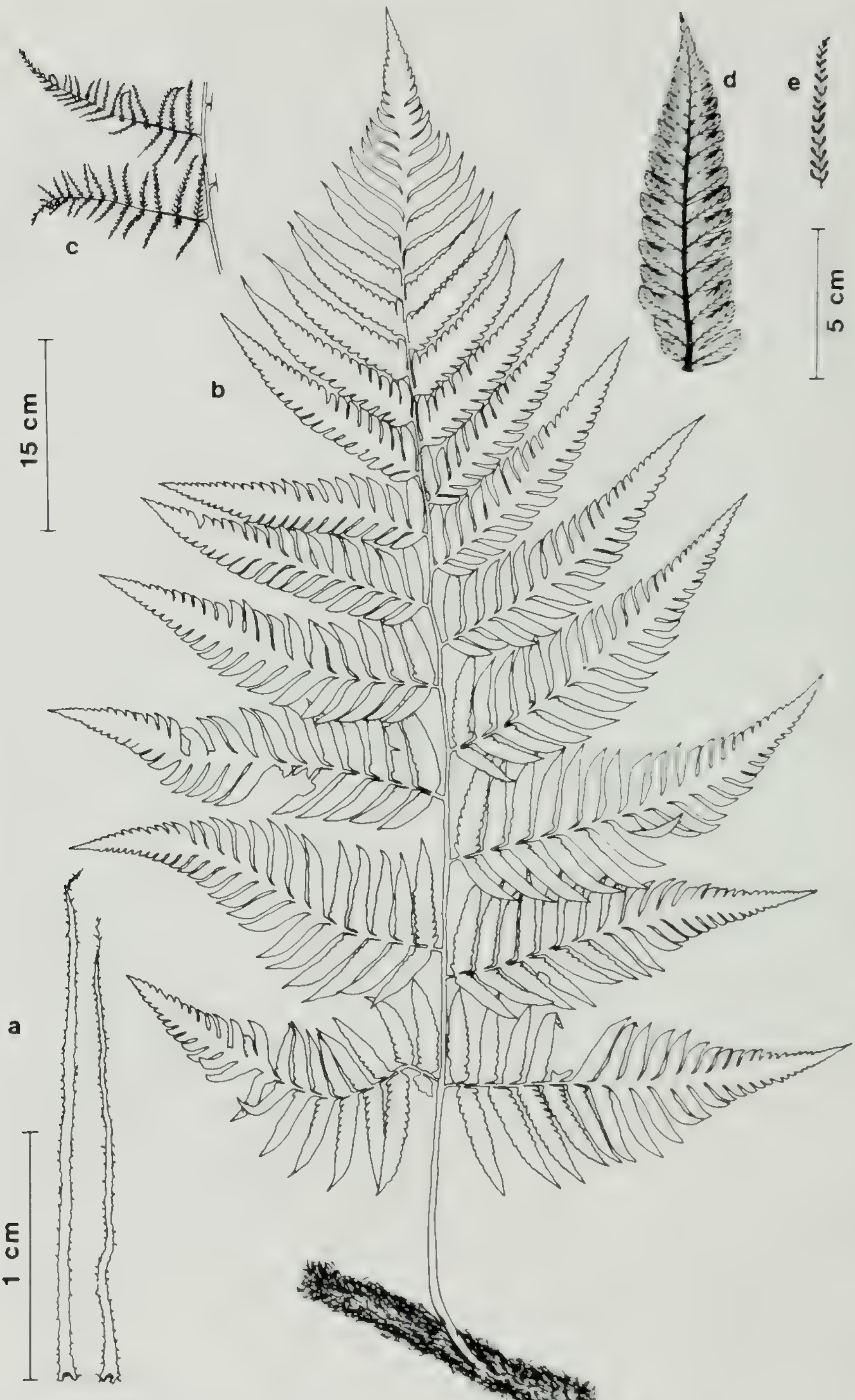

FIGURE 45. *Polybotrya altescandens* C. Chr. a. stem scales; b. fertile leaf; c. fertile pinnae; d. sterile pinnule (note isolated veinlet between the main pinnate groups); e. fertile pinnule (note obovate segments). a,b: *Moran 3559* (CR). c,e: *Rimbach 91* (F). d: *Steyermark 52812* (F).

and Peru (Map 12). I suspect that this species occurs in many other valleys of the Colombian and Peruvian Andes, and that lack of collecting accounts for the apparent disjunctions. My field experience in Ecuador showed this species to be quite common in the western cordillera but absent from the eastern cordillera.

Polybotrya altescandens can be immediately recognized by its bright golden to yellowish scales that thickly cover the stem. These scales are longer and narrower than those of any other species of *Polybotrya* (Fig. 45a). The lamina is less cut than that of similar Andean species, and the pinnae soon become pinnatifid in their distal portions, a characteristic that further accentuates this less-divided look. The sori are usually clavate or short-oblong, in contrast to the more elongated sori of other species (Fig. 45e). An unusual tendency of the venation further distinguishes this species: in large pinnae and pinnules the lowermost basiscopic vein migrates onto the costa or costule and therefore appears as a single isolated veinlet between the main pinnate groups (Fig. 45d).

Specimens examined: COLOMBIA. **Antioquia:** bosque bajo la cumbre cerca de Boquerón, camino entre Medellín y Palmitas, 2300–2500 m, *Hodge 6592* (GH).

ECUADOR. **Azuay:** rich dense jungle between Chacanceo and Río Blanco, on road to Molleturo, between Río Putucay and Río Norcay, 1220 m, *Steyermark 52812* (F). **Carchi:** environs of Maldonado, 1450 m, *Madison et al. 4851* (F). **Chimborazo:** mountains in Sacramento area, *Wiggins 11073* (NY). **Cotopaxi:** road between Quevedo and El Corazón, 6.4 km NW of El Corazón, 67.5 km SE of Quevedo, *Croat 55844* (MO). **Guayas:** valley of Río Chimbo, 800 m, *Rimbach 91* (F, US). **Imababura:** in the vicinity of the Río Verge, ca. 5 km SW from the village of Mani, Río Cachaco, 1300 m, *Sperling & Bleiweiss 5034* (GH, Q, QCA). **Pichincha:** tropical forest de Pilaton-Toachi, September 1892, *Sodiro s.n.* (P); road El Paraiso–Saguangal, 11 km from El Paraiso, *Øllgaard et al. 37702* (AAU), *37867* (AAU); road El Paraiso–Saguangal, 3 km from El Paraiso, 1500 m, *Øllgaard et al. 37820* (AAU); selva topical, Valle de Nanegal, *Sodiro s.n.* (P, US); Mindo, *Sydow 339* (US); road from Sto. Domingo de los Colorados to Aloag, 2.5 km E of Cornejo Astorga, 1200 m, *Moran 3544* (F, GH, Q, QCA); Tinalandia Resort, ca. 25 km E of Sto. Domingo de los Colorados, N side of Río Toachi, 1000 m, *Moran 3559* (CR, F, GH, NY, Q, QCA); ca. 30 km WNW of Quito, 67 km on road to Mindo, 2200 m, *Moran 3564* (F, Q, QCA, US). **Province unknown:** western cordillera, 800 m, forest region, *Rimbach 312* (US); without locality, *Jameson 33* (P).

PERU. **Huánuco:** La Divisoria, ca. 25 km NE of Tingo María, *Moran 3688* (F, GH, MO, USM). **Loreto:** Prov. Coronel Portillos, Dtto. Padre Abad., divisoria cerca al Río Chino, *J. Schunke 10200* (MO).

27. Polybotrya gomezii Moran, *sp. nov.* (Fig. 46, Map 14).

Polybotrya gomezii Moran, *sp. nov.* TYPE: Costa Rica. Alajuela: ca. 20 km N of San Ramón, at the Univ. of San Ramón's Biological Field Station, 1100 m, cloud forest, 17 July 1983, *Moran 3241* (holotype: CR!; isotypes: F!, GH!, MO!, NY!, UC!, US!).

Caulis hemiepiphyticus, 1–2 cm diam.; squamae appressae vel ascendentes, brunneae, obscurae, opacae, anguste lanceolatae, vulgo 10–20 × 1–2 mm, marginibus vulgo integris; lamina usque ad 1.5 × 0.75 m, ovata vel deltata, admodum glabra, 2-pinnata-pinnatifida, coriacea, inferne anadromica, superne catadromica; pinnae usque ad 45 × 20 cm, anguste deltatae, apicibus longiacuminatis; pinnulae usque ad 12 × 2.5 cm, acroscopice leviter prolongata. Folia fertilia usque ad 0.75 m, 3-pinnata; sporae (50)54–60(64) micrometralae.

Stem 1–2 cm thick, hemiepiphytic; *scales* appressed to spreading, dull brown, opaque, thickened in the middle, narrowly lanceolate, 10–20 × 1–2 mm, margins entire or with a few apical denticulations. *Sterile leaf* up to 1.5 m long; *lamina* up to 1.2 × 0.75 m, 2-pinnate-pinnatifid or very rarely 3-pinnate, coriaceous, ovate-triangular, nearly glabrous, usually anadromic below, becoming catadromic in the distal one-third, the change from anadromic to catadromic marked by a small, reduced, basiscopic pinnule or segment; *pinnae* up to 45 × 20 cm, narrowly triangular, the apex long acuminate, the lower ones pinnatifid in the apical third, giving a broadened appearance to the pinnae; *pinnules* up to 12 × 2.5 cm, apex of proximal ones acuminate to long acuminate, gradually becoming curved and then truncate in the pinnatifid apex, the base inequilateral with the acroscopic side slightly more developed, the margins serrate to pinnatifid; *axes* usually glabrous abaxially or with unicellular, fine, whitish hairs, scaly, the scales caducous, appressed, up to 2 mm long, light brown, with a long narrow apex; *grooves* mostly glabrous within or nearly so, sometimes

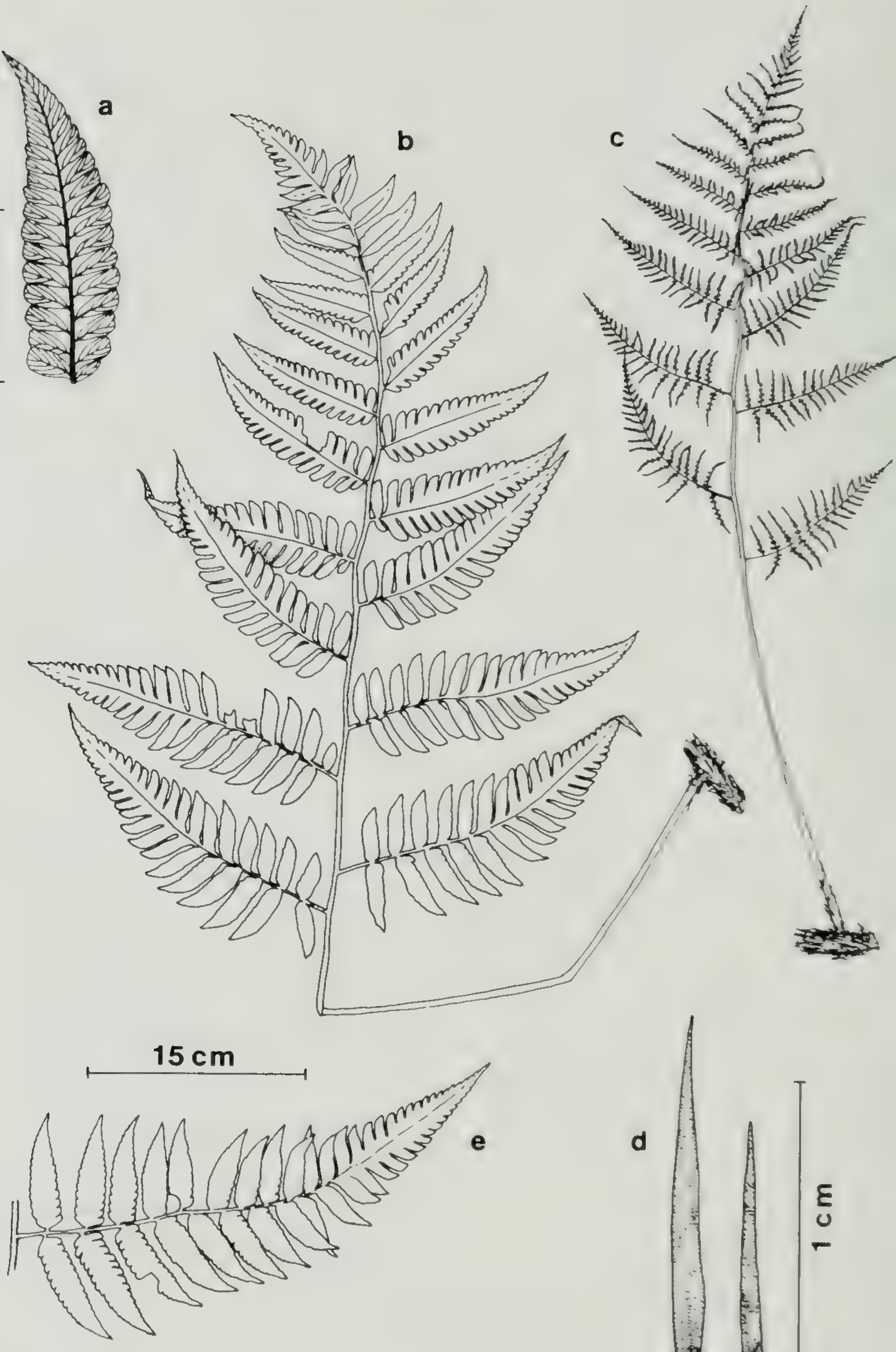

FIGURE 46. *Polybotrya gomezii* Moran. a. acroscopic basal pinnule, pinnae apex toward the left (note catadromous venation); b. sterile leaf (note that the transition zone from anadromic to catadromic is marked by reduced basiscopic pinnules); c. fertile leaf; d. stem scales; e. basal pinna. a,d: *Moran 3241* (CR). b,e: *Moran 2441* (F). c: *Lent 3537* (F).

pubescent at the junctures, the hairs short, less than 0.1 mm long and inconspicuous. *Fertile leaves* up to 0.75 m long, 3-pinnate, coenosoric; *axes* with scattered scales similar to those on the sterile leaf, junctures pubescent, the hairs numerous, short, less than 0.2 mm long; *sporangial stalks* paraphysate; *spores* (50)54–60(64) microns long.

This species is named in honor of Luis D. Gómez P., pteridologist, formerly at the Museo Nacional de Costa Rica, who has encouraged my study of *Polybotrya* and extended much hospitality during my thesis research in Costa Rica. *Polybotrya gomezii* is endemic to Costa Rica (Map 14), where it occurs from sea level up to 1500 m, reaching its greatest frequency and abundance in cloud forests. Most of the specimens were collected in the mountains around San José. I found *P. gomezii* at five localities, always with *P. alfredii*; no hybrids were found.

This species can be distinguished from others in Central America by its nearly glabrous, only 2-pinnate-pinnatifid leaves, and the nearly glabrous axes. The pinnae soon become pinnatifid in the apical half, which also gives a more broad, less finely cut appearance to the leaf (Fig. 46b). The opaque, dull brown stem scales with entire or sparsely denticulate margins (Fig. 46d) also help separate this species from others found in Costa Rica. The veinlets of the pinnules are always arranged catadromically, even in pinnae having the pinnules arranged anadromically. This ordering is unusual because the disposition of the veinlets usually reflects the pinnule arrangement; that is, if the pinnules are anadromic, the veinlets are also anadromic.

Specimens examined: COSTA RICA. **Alajuela:** ca. 20 km N of San Ramón, at the Univ. of San Ramón's Biological Field Station, cloud forest, *Moran 3241* (CR, F, GH, MO, NY, UC, US); forest between Quebrada Quicuyal and Quebrada Arrayanes, Cariblanco, *Lent 3537* (F). **Cartago:** near Alto Patillos, *Moran 2441* (CR, F, GH, MO, NY, US); cloud forest near the entrance to Parque Nacional Tapantí, 1270 m, *Moran 3338* (CR, F, GH, NY, US); 3 km SE of Tapantí, lower slopes of Alto Patillos, *Lent 1084* (F); La Hondura, 1400 m, *Valerio s.n.*, (CR); Navarro, 1400 m, *Wercklé s.n.* (GH, P). **Heredia:** about 10 km on the road towards Virgen de Socorro, 1000 m, *Moran 3160* (CR). **Puntarenas:** Monteverde Cloud Forest Reserve, 1560 m, *Fiedler & Koptur 51* (UC). **San José:** Parque Nacional Braulio Carrillo, ca. 1 km along road from entrance, *Moran 3271* (CR).

28. Polybotrya osmundacea Willd. (Figs. 47 & 48, Map 18).

Polybotrya osmundacea Willd., Species Pl., ed. 4, 5:99. 1810. TYPE: Venezuela. Monagas: Caripe, *Humboldt 459a* (fertile), *459b* (sterile), Herb. Willd. 19507-1, 19507-2 (holotype: B; photos F!, GH!).

Acrostichum osmundaceum (Willd.) Hooker, Species Filicum 5:246. 1864.

Polybotrya aristeguietae Brade, Bradea 1:19, tab. 1. 1969. TYPE: Venezuela. Miranda: Santa Teresa-Altogracia de Orituco, June 1953, *Aristeguieta 1780* (holotype: VEN!).

Polybotrya vareschii Brade, Bradea 1:20, tab. 2. 1969. TYPE: Venezuela. Aragua: Rancho Grande, Dependiente Norte, selva nublada, 800 m, *Vareschi & Gessner 1875* (holotype: VEN!).

Stem 1–2.5(4) cm thick, hemiepiphytic; *scales* extremely variable, with plants from Amazonia tending to have thick, opaque, dark brown, subentire, somewhat squarrose scales and plants from elsewhere tending to have shiny, ascending, spreading, bicolorous scales, often with a dark central stripe and lighter borders, margins highly erose or, less commonly, denticulate, mostly 1.0–2.2 × 0.8–1.9(2.3) cm. *Sterile leaves* up to 1.8 m long; *lamina* deltate, ovate, or lanceolate, to 3-pinnate-pinnatifid, chartaceous, rarely with scattered, round, sessile, resinous glands on the abaxial surface, the margins glabrous; *pinnae* narrowly deltate, equilateral, (7)13–18 pairs; *pinnules* arranged anadromically or rarely catadromically (Peru), up to 14 × 4 cm, the largest deeply cut at the base, apex acuminate; *basal acroscopic tertiary segments* ovate, lanceolate or rhombic, margins entire, crenate or lobed, the apex often serrulate; *axes* glabrous or pubescent abaxially, the hairs whitish, 0.2–0.5 mm long, the scales absent or few and inconspicuous; *grooves* decurrent into those of the next lower order, usually filled with short, less than 0.7 mm long, reddish or brownish hairs. *Fertile leaves* to 3-pinnate-pinnatifid, deltate, coenosoric; *sporangial stalks* paraphysate; *spores* (50)54–62(66) microns long.

Other illustrations: See original descriptions of *P. aristeguietae* and *P. vareschii*; Humboldt et al., Nov. Gen. Sp. Pl., tab. 2. 1815; Proctor, Ferns of Jamaica, fig. 107. 1985.

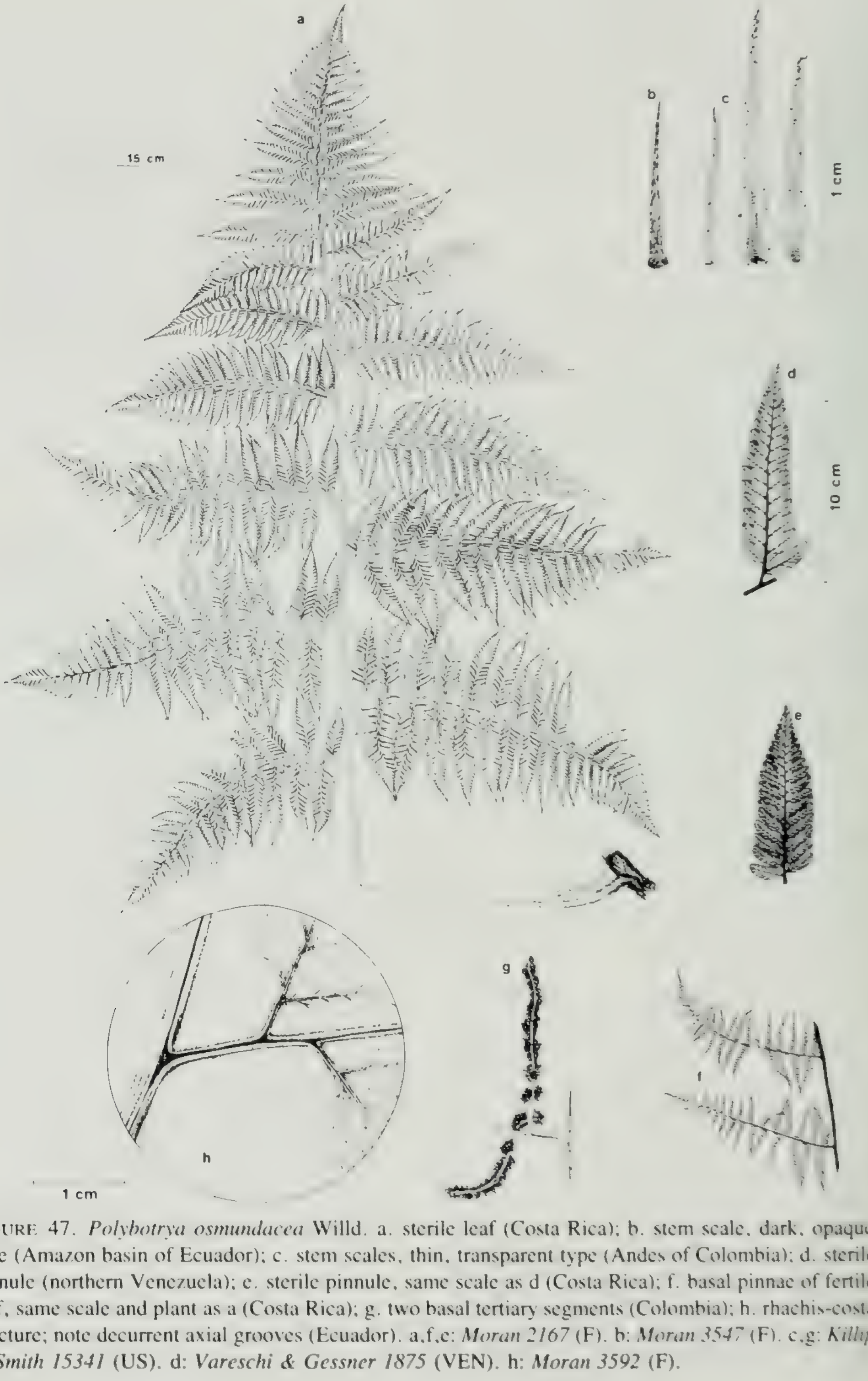

FIGURE 47. *Polybotrya osmundacea* Willd. a. sterile leaf (Costa Rica); b. stem scale, dark, opaque type (Amazon basin of Ecuador); c. stem scales, thin, transparent type (Andes of Colombia); d. sterile pinnule (northern Venezuela); e. sterile pinnule, same scale as d (Costa Rica); f. basal pinnae of fertile leaf, same scale and plant as a (Costa Rica); g. two basal tertiary segments (Colombia); h. rhachis-costa juncture; note decurrent axial grooves (Ecuador). a,f,e: *Moran 2167* (F). b: *Moran 3547* (F). c,g: *Killip & Smith 15341* (US). d: *Vareschi & Gessner 1875* (VEN). h: *Moran 3592* (F).

Polybotrya osmundacea, the type species of the genus, is one of the most widely distributed species of *Polybotrya* (Map 18). It occurs in wet, shaded forests from sea level to 2100 m. The specific epithet refers to the fancied resemblance of the fertile leaves to the fertile apex of *Osmunda regalis* (Willdenow 1810).

This species varies tremendously in scales, cutting, and pubescence. In plants from Amazonia, the scales are usually thick, dark, opaque, more or less squarrose, and not thickly investing the stem so that the yellowish stem aerophores are easily visible in fresh material (Fig. 47b). Plants from other parts of the range may be similar, but more often the scales are thin, lighter colored, transparent, often bicolorous, and more thickly investing the stem (Fig. 47c). The stem scales, however, do not correlate with any other characteristics.

Laminar cutting is another variable characteristic. The type specimens of *P. aristeguietae* and *P. vareschii*, both collected in northern Ven-

FIGURE 48. Geographical variation in the pinnule cutting of *Polybotrya osmundacea* Willd. The elongated side of the pinnule is always acroscopic. Clockwise, starting from Bolivia: *Buchtien 298* (UC); *Killip & Smith 23991* (F); *Moran 3642* (F); *Moran 3618* (PORT); *Lellinger & de la Sota 213* (COL); *Moran 2167* (CR); *H. Smith 1050* (US); *Vareschi & Pannier 1686* (US); *Killip & Lasser 37756* (US); *Murillo 2580* (F); *Broadway 5589* (F); *Steyermark 107148* (MO); *Granville 3865* (CAY); *Berg et al. P18138* (NY).

ezuela, scarcely differ from each other in cutting. These two specimens, however, seem to differ from *P. osmundacea* elsewhere in its range by their less-cut leaves (Fig. 47d; Fig. 48, pinnules from northern Venezuela). From the greater number of specimens available to me, it appears that these extremes of cutting are connected by intermediates and that no other characters correlate with these extremes. Accordingly, I have placed *P. aristeguietae* and *P. vareschii* in synonymy with *P. osmundacea*.

Specimens examined: GUATEMALA. **Izabal:** vicinity of Quiriguá, *Standley 24195* (NY, US).

HONDURAS. **Prov. unknown:** near Lake Yojoa, *Steeves & Ray 504* (GH, US); near Cockscomb Mts., *Schipp 8101* (US); Maya Mounds, *Schipp 8108* (F).

NICARAGUA. **Comarca del Cabo:** 40–50 km SW of Waspán, *Atwood 3711* (VT). **Zelaya:** Cerro la Pimienta, no. 1, summit area, *Pipoly 5146* (CR); costado S del Cerro La Pimienta, *Grijalva 300* (CR).

COSTA RICA. **Cartago:** forests of Las Vueltas, Tucurrique, *Tonduz 13337* (US), *18879* (US); forests of Tuis, *Pittier 12416* (CR, US); Aragón, *Pittier 9076* (Z); Chitaría, *Valerio 328* (US); Chitaría, forest near old jailhouse, *Moran 2167* (CR, F); Turrialba, Aragon, *Tonduz 9006* (US), *9016* (US); vicinity of Pejivalle, *Skutch 4637* (CR, US); Peralta, *Lankester s.n.* (US); vicinity of Pejivalle, *Standley & Valerio 47127* (US); Turrialba, Instituto Interamericana, Ganadería, *Croat 690* (MO), *738* (MO); Florecia, Turrialba, *Jiménez 3299* (F), *3304* (CR, F); Reventazón below Turrialba, *Hatch 90* (F); Turrialba, *Pittier 9016* (Z); 3 km W of Turrialba, *Mickel 2624* (LP, NY); Turrialba, near the Interamerican Inst., *Scamman 7152* (GH), *7687* (GH); Turrialba, *Lent 299* (GH); valley of Río Reventazón, 3 km SE of Turrialba, *Holm & Iltis 200* (MICH). **Cocos Island:** *Stewart 241* (US); *Fisher s.n.* (US); *Klawe 1474* (US), *1504* (US). **Limón:** SW of Siquirres, on road to Turrialba between Moravia and Guayacán 1 km of Guayacán, *Lellinger & White 1436* (F, US); near banana plantation and Pandora, Río Estrella, *Rossbach 3628* (GH); Los Diamantes, USDA Rubber Plant Station, *Scamman 5987* (GH), *7153* (GH); hills of Atlantic slope, *Tonduz 14568* (P); vicinity of Guápiles, *Standley 37096* (US). **Puntarenas:** Coto, at sea level, *Valerio 333* (F); San Vito, *de la Sota 5181* (LP); Finca Loma Linda 1 mi SW of Cañas Gordas, *Croat 22260* (MO); road to Puerto Jimènez, Osa, 40 km W of I.A. route 2, *Gómez 19489* (CR, UC); Osa Peninsula, 15 km S of Tropical Science Center field station and ca. 20 km S of Rincón de Osa, *Mickel 2803* (NY), *2817* (NY); Finca Las Cruces, San Vito de Java, *Burch 4613* (MO, NY); ca. 10 mi. SE of Rincón de Osa along road to Pacific, *Evans & Bowers 2792* (MO). **San José:** vicinity of El General, *Skutch 3018* (F, MO); San Isidro de El General, *Scamman 5984* (GH).

PANAMA. **Chiriquí:** 10–11 miles W of Puerto Armuelles in vicinity of San Bartolo Limite, *Croat 21987* (MO); vicinity of Gualaca ca. 10.7 miles from Planes de Hornito, La Fortuna on road to dam site, *Antonio 5133* (MO, UC); 4.5–5.0 km N of dam over Fortuna Lake, *Croat & Grayum 60022* (MO); Fortuna Dam area, Quabrada Bonito to N of reservoir, *Churchill 5776* (MO). **Darién:** vicinity of airstrip at Caña gold mine, *Croat 38047* (MO). **Panamá:** Cerro Jefe, near summit, *Croat 22682 (MO)*.

CUBA. **Oriente:** Sierra Maestra on ascent from Río Yara, *Ekman 14210* (US); Bahía de Taco, on the ridge below Santa María and Río Jiguaní on the path to the "Iberia" mines, *Ekman 3769* (NY); Trail Navas to Camp Buena Vista, *Shafer 4458* (NY); La Perla, *Maurel & Maurel 3816* (NY); La Perla, *Shafer 8889* (NY); near Monte Verde, *Wright 786* (BM, F, GH, MO, NY, PH, UC, US); *Eggers 5324* (F); Finca Guadalupe, Placetas, Las Villas, *Acuña 17531* (US); Sevilla Estate, near Santiago, trail from Magdalena to Sierra Maestra, *Taylor 447* (NY); Loma del Gato and vicinity, Sierra Maestra, *Hioram & Clement 6424* (GH, US); La Prenda, *Hioram 2495* (COL, P, US, UC); Santiago, Loma del Gato-Cobre, *Clement 725* (US).

JAMAICA. **Clarendon:** "Second Breakfast Spring" below Tweedside, *Underwood 1612* (NY). **Portland:** Dollwood, *Watt 160* (GH, P, US), *7276* (BM); Mabess River, below Vinegar Hill, *Underwood 1323* (NY); trail from Vinegar Hill to Mabess River, *Underwood 1246* (NY), *1250* (NY); Mabess, *Fisher 132* (NY); Blue Mts., Stony River to Macungo River, *Morely & Whitefoord 655* (BM), *675* (BM); Blue Mts., Stony River Base Camp, *Morely & Whitefoord 695* (BM, MO); John Crow Mts., E slope, 1.5 mi SW of Ecclesdown, *Wilson & Webster 549* (MICH); above Moore Town, *Clute 259* (NY, US); valley of the Río Grande, 8 air miles S of Port Antonio, *Gastony 43* (GH); vicinity of Thomsons Gap, *Maxon & Killip 756* (F, GH, NY, US); Spur of John Crow Mts. opposite Mill Bank, *Maxon 9366* (GH, NY, PH); vicinity of Mill Bank, *Maxon & Killip 148* (F, GH, NY, US); along trail to waterfall N of Hardwar Gap, *Proctor 16506* (MO), *22269* (GH). **St. Andrew:** Blue Mts. near Cinchona, 15 km from Kingston, *Fisher s.n.* (P); Catherine Peak, *Faull 12583* (GH). **St. Ann:** Blue Mts., Trafalgar, *Perkins 1163* (GH). **St. Catharine:** vicinity of Hollymount, Mount Diablo, *Maxon 2293* (NY, US). **St. Thomas:**Mansfield and adjoining properties, near Bath, *Maxon 2470* (NY, US); Manchester Blue Mt., *Day s.n.* (NY); forested ridge E of Cuna Cuna Gap, *Maxon 9464* (NY, US); Bath, *Gilbert s.n.* (GH); upper southern slopes and summit of Maccasucker Bump, *Maxon 9522* (GH, NY, PH); SE slopes of Stone Hole Bump, *Maxon 8978* (GH, NY, PH); Corn Puss Gap and vicinity, trail W over Blue Mts., *Wilson & Murray 564* (BM, GH, MICH); Corn Puss Gap, *Proctor 3969* (PH, US).

HAITI. Massíf du Nord, Chavary, *Ekman 4734* (US); Camp Perrin, *Ekman 5214* (US).

GRENADA. Grand Etang, *Beard 1252* (UC, US); no locality, *Fraser s.n.* (P); in Mirabeau Mts., *Broadway*

2520 (Z); St. Georges, Azimas, 1896, *Broadway s.n.* (NY); without locality, *Sherring 13* (BM).

TRINIDAD. Pass, Arima Valley, *Fleming & Fleming 52* (NY); no locality, *Fendler 69* (BM, F, GH, MICH, MO, NY, P, PH, UC); *Hart 229* (P); Mount Tocuche, *Britton et al. 1267* (GH, NY, US); Tacarigua Ward, El Tocuche, *Walker T10995* (BM); Morne Bleu, *Britton et al. 2276* (GH, NY, US); St. George, Blanchisseuse, Las Lapas trace, *Barnard et al. 411* (BM, MO); Blanchisseuse saddle, *Richardson 2037* (US); Blanchisseuse road, 11-mile post, *Broadway 6902* (F, MO, Z); Blanchisseuse road, 10-mile post, *Broadway 5589* (F, MO); Heights of Aripo, *Broadway 9948* (F, NY, US), *9950* (F, GH, NY, US), *9951* (GH, NY, US); Las Lapas road, *Broadway 6459* (BM); Arima–Blanchisseuse road, 13-mile post, *Jermy 11195* (BM), 9-10-mile post, *Jermy 2368* (BM); Morne Bleu ridge, *Jermy 2846* (BM); Arima–Blanchisseuse road, 10-mile post, *Fay 373* (BM); Maracas Valley, Las Cuevas trail, *Fay 345* (BM); 10.5 mi N of Arima, *Crosby 76* (MICH).

FRENCH GUIANA. Sommet tabulaire, zone centrale, about 40 km SE of Saul, *Granville 3865* (CAY, Z).

GUYANA. Region of Mt. Raywa, *Jenman s.n.* (NY).

VENEZUELA. **Anzoátegui:** Dtto. Bolívar, Fila El Gácharo, ridge of the fila above Los Chorros and El Cielo, Serranía de Turumiquire, *Davidse & González 19444* (MO). **Apure:** Reserva Forestal San Camilo, SW of caserío San Camilo (El Nula), *Steyermark et al. 101552* (US, VEN). **Aragua:** selva nublada de Rancho Grande, Dependiente Norte, *Vareschi & Gessner 1875* (VEN); Parque Nacional, Dos Ritos, *Killip & Lasser 37756* (US, VEN). **Barinas:** Dtto. Bolívar, along road from Barinitas to Mérida, near one land bridge at San Isidro, 30 km NW of Barinitas, *Moran 3718* (PORT, VEN); Dtto. Bolívar, San Isidro, ca. 5 mi NW of La Soledad along Barinas–Sto. Domingo road, *A.R. Smith et al. 1388* (PORT, UC, Z). **Distrito Federal:** virgin wet forest on slopes along old road between "Portachuelo" and "Penita" (Petaquire) and Carayaca, between Colonia Tovar–Junquito road and Hacienda El Limón, 6–8 mi below junction of Junquito–Colonia Tovar road, *Steyermark & Nevling 95930* (GH, VEN). **Falcón:** Cerro Azul, *Wingfield 6914* (VEN). **Falcón/Lara:** Cerro Socopa, *Liesner et al. 8359* (MO, VEN). **Lara/Yaracuy:** Dtto. Urdaneta y Bolívar, la fila Azul y Hda. El Jaguar, *Ortega & Smith 2387* (PORT); Sierra de Aroa, 10–13 mi NW of Urachiche (Edo. Yaracuy) along dirt road leading NW from Urachiche to Duaca (Edo. Lara), *A.R. Smith et al. 1347* (UC, PORT, Z). **Miranda:** Santa Teresa–Altogracia de Orituco, *Aristeguieta 1780* (VEN); Cerros del Bachiller, near E end of virgin evergreen forest, above Quebrada Corozal, S of Santa Cruz, 10 km (by air) W of Cupira, *Steyermark & Davidse 116499* (MO, UC, VEN). **Monagas:** Caripe, *Humboldt 459a,b* (P, photo F, GH); Cerro de Gáucharo, of Guácharo, *Steyermark 62015* (F). **Nueva Esparta:** Cerro Copey, *Sugden 1151* (UC). **Territorio Federal Amazonas:** Sierra Parima, vecinidades de Simarawochi, Río Matacuni, a unos 6–7 km al oeste de la frontera Venezolana–Brasilera, *Steyermark 107148* (MO, NY, VEN); Depto. Río Negro, 0–2 km E of Cerro La Neblina Base Camp on Río Mawarinuma, *Liesner 16133* (MO, UC); environs of Neblina Base Camp, *Plowman & Thomas 13678* (F, UC). **Sucre:** Península de Paria, Dtto. Mariño, camino Mundo Nuevo–Manacal, 18–20 km N de Irapa, *Dumont et al. 7439* (NY, VEN); alrededore de Manacal, *Murillo 2580* (F, NY, VEN); Península de Paria, Cerro de Humo, NE de Irapa, *Steyermark 94952* (F, GH, VEN); Península de Paria, arriba de Mundo Nuevo, oeste de Cerro de Humo, *Steyermark & Rabe 96145* (GH, VEN); Península de Paria, vicinity of Manacal 15 km (by air) NW of Irapa, *Steyermark & Liesner 120634* (MO, UC, VEN); Península de Paria, arriba de Mundo Nuevo, oeste de Cerro de Humo, *Steyermark & Rabe 71756* (VEN). **Táchira:** Dtto. Uribante, along road from La Siberia to entrance to Las Cuevas Represa, *van der Werff & González 5202* (MO, UC). **Yaracuy:** Dtto. Bruzual, selva siempreverde, Montaña de María Lionoza, Quebrada Quibayo, desde abajo hasta casi la cumbre, *Steyermark et al. 125039* (UC, VEN); Cerro "Chimborazo," Sierra de Aroa, *Vareschi & Pannier 2715* (US, VEN); en la selva que cubre la fila "La Enjalma" al sur de Chivacoa, *Vareschi & Pannier 2660* (VEN). **Zulia:** Parija, *Vareschi 3147* (VEN); Dist. Mara, NW wooded slopes of Cerro Negro, 5.5 km SW of Rancho 505, S of Río Guasare, *Steyermark et al. 122814* (MO, VEN); Dtto. Bolívar, Cuenca del Embalse Burro Negro (Pueblo Viejo), sector entre Quiros–El Pensado y el pie de Cerro Socopo, en el área aprox. 10 km en línea recta al este de Churugauarita, *Bunting 9516* (VEN); 15 km de El Vigía, carretera Panamericana, *Vareschi & Pannier 1686* (US).

COLOMBIA. **Antioquia:** Río Leon, Bendix site, *Cain 74* (MICH); carretera al mar cerca de Villa Arteaga, *Gutiérrez & Barkley 170109* (GH); Municip. Anori, Providencia, *Soejarto 2805* (COL). **Boyacá:** Muzo, *Lindsay 262* (BM). **Cauca:** Agua Clara, along hwy from Buenaventurea to Cali, *Killip & Cuatrecasas 38902* (F, US); Costa del Pacífico, Río Micay, brazo Noanamito, orilla derecha, El Chachajo, *Cuatrecasas 14246* (US). **Chocó:** 0.5–2.5 km N of the INDERENA Camp on Río Truando near Caserío La Teresita, *Lellinger & de la Sota 553* (COL, US); NW side of Alto del Buey, *Lellinger & de la Sota 213* (COL, US), *250* (COL, LP, US); trail from Río Mecana to Alto de Mecana, *Gentry & Juncosa 41021* (MO, UC). **Magdalena:** Sierra Nevada de Santa Marta, región del Campano, *Barkley & Gutiérrez V. 1897* (MICH); Santa Marta, near Las Partidas, 3500 ft, *H.H. Smith 1050* (B, F, NY, MICH, MO, PH, US, VT); Forest Boca Toma, El Recuerdo, 2500 ft, *Bennett 23* (F); Santa Marta Mts., trail beyond falls, El Recuerdo, *Niemeyer 44* (US). **Meta:** Villavicencio, *Alston 7641* (BM). **Santander:** Barbosa, *Henri-Stanislas 1710* (US); Mesa de los Santos, *Killip & Smith 15341* (COL, GH, NY, US); between Lebrija and San Vicente, *Alston 7341*

(BM). **Prov. unknown:** Municip. de Marsella, Vereda La Nona, Finca Palermo, cerca al caserío Caracas, Cordillera Central, vertiente occidental, *Idrobo et al. 10116* (COL).

ECUADOR. **Los Ríos:** Río Palenque Biological Station, km marker 56 N of Quevedo, *Moran 3600* (Q, QCA). **Napo:** 27 km SE de Coca, alrededor de pozo de petroleo Auca 4, *Moran 3618* (PORT, Q, QCA); 12 km SW of Coca, por el camino se llama "Los Zorros," *Moran 3612* (Q, QCA); 73 km NE de Baeza, propiedad de Inecel, "Cascada de San Rafael," *Moran 3592* (F, MO, Q, QCA); Puerto Francisco de Orellana (Coca), 17 km SW of the town at road along Río Napo (Los Zorros), *Balslev & Madsen 10649* (AAU, Q, QCA); Río Napo, Pañachocha (Oasis), *Harling et al. 7535* (F, GH); Añangu, Parque Nacional Yasuni, SEF project area, *Øllgaard et al. 38845* (AAU, Q, QCA), *38894* (AAU, Q, QCA), *39086* (AAU, Q, QCA). **Pastaza:** Lorocachi, zone oeste del campamento militar a 3 km del Río Curaray, *Jaramillo et al. 30783* (AAU, Q, QCA). **Pichincha:** Pululahua, *Sodiro s.n.* (US); Chimborazo, *Spruce 5685* (P); Los Colorados, *Sodiro s.n.* (P); 15 km E of Sto. Domingo de los Colorados, road behind Brasilia a Toachi, along Río Toachi, *Moran 3547* (F, Q, QCA). **Santiago-Zamora:** Cordillera Cutucú, ridge just S and W of Río Itzintza, *Camp 1298* (NY), *1359* (NY). **Tungurahua:** Baños-Jivaria de Pintuc, *Stübel 875* (B). **Prov. unknown:** Junganza, *Crespi s.n.* (US); San Miguel, *Sodiro 81* (UC).

PERU. **Huánuco:** SW slope of the Río Llulla Pichis watershed, on the ascent of Cerros del Sira, Camp 3 (Laguna), *Dudley 13005* (GH); Tingo María, *Allard 21609* (US), *21997* (US). **Junín:** Pichis Trail, Yapas, *Killip & Smith 25452* (NY, US); Chanchamayo Valley, *C. Schunke 164* (F), *705* (F), *1341* (F), *1395* (F), *1451* (F); E of Quimiri bridge, near La Merced, *Killip & Smith 23991* (F, NY, US). **Loreto:** Prov. Maynas, Peter Jensen's Explorama Lodge, 50 mi downriver on the Amazon at Yonamono Ck., *Moran 3642* (AMAZ, F, USM); Altura Tuta Pishco on Río Napo, *Croat 20287* (MO); Gamitanacocha, Río Mazán, *J. Schunke 275* (F, GH, NY, UC, US), *380* (F, GH, UC, US); Pumayacu, between Balsapuerto and Moyobamba, *Klug 3208* (F, GH, MO, US); Veradera de Mazàn, *Croat 20786* (MO); 17 km SW of Iquitos, *Croat 18476* (MO); Río Napo near Entrada de Isla Inayuga, *Croat 20543* (MO). **Madre de Dios:** Prov. Manu, *Vargas 17743* (GH). **San Martín:** Camino a Pushurumbo, 7–8 km E del puente de Palo Blanco, Mariscal Caceres, Tocache Nuevo, *J. Schunke 5785* (COL, NY, US). **Ucayali:** Río Aguaytia above mouth of Quebrada Yurac–Yacu, *Croat 20851* (MO).

BOLIVIA. **La Paz:** Región de Mapiri, *Buchtien 298* (NY, UC, US); Mapiri, San Carlos, *Buchtien 1066* (LP); Yungas, Mururata, 1839, *Pentland s.n.* (P).

BRAZIL. **Amazonas:** Manaus–Caracarai road, km. 148, *Berg et al. P18138* (F, NY, VEN). **Pará:** Serra dos Carajás, AMAZ Camp Azul, *Sperling et al. 5915* (GH, NY).

29. Polybotrya cyathifolia Fée (Fig. 49, Map 19).

Polybotrya cyathifolia Fée, Mém. Fam. Foug. 6. (Hist. Acrost.) tab. 2. 1866. TYPE: Guadeloupe. "near the house of Mr. Bovie," *L'Herminier s.n.* (holotype: P!; other L'Herminier specimens that are probably types are at GH!, L!, fragment NY!).

Stem 1–2 cm thick, hemiepiphytic; *scales* dull, light reddish brown, concolorous, spreading, the margins subentire to denticulate. *Sterile leaves* up to 1.5 m long; *lamina* to 3-pinnate, ovate to lanceolate, up to 1.2 × 0.8 m, membranaceous, almost always with round, sessile, reddish, punctate glands; *pinnae* up to 40 × 23 cm, narrowly deltate, pinnatifid to the very apex, stalked 5–10 mm; *pinnules* catadromous to anadromous but mostly subequal, narrowly deltate, stalked 1–3 mm, the base subequilateral, slightly prolonged acroscopically but not oblique or cuneate on the basiscopic side; *tertiary segments* serrate to entire, the proximal ones of the largest pinnules oblong, slightly gibbous at the base on both the basiscopic and acroscopic sides; *axes* abaxially sparsely to moderately pilose with hairs similar to those above; *grooves* densely packed with multicellular reddish or tawny hairs, these 0.3–0.8 mm long and conspicuously exserted from the groove, evident to the unaided eye, especially at the pinnae junctures. *Fertile leaves* 3-pinnate-pinnatifid, coenosoric; *sporangial stalks* paraphysate; *spores* (47)50–59(63) microns long.

Other illustrations: See original description; Plumier, Tr. Foug. Amér. tab. 32. 1705.

Polybotrya cyathifolia is endemic to the Caribbean islands of Guadeloupe and Martinique (Map 19). Few collections have been made of this fern, but the original collection by L'Herminier is well prepared and has many duplicates.

Polybotrya cyathifolia is very much like *P. osmundacea*, but it differs by the shape of its tertiary segments, the resinous punctate glands, and by the long-pilose hairs on the axes. The best way to distinguish *P. cyathifolia* is by the costal groove hairs that copiously fill and protrude from the groove, especially at the junctures (Fig. 49c). *Polybotrya osmundacea*, on the other hand, usually has very short hairs (0.1–0.2 mm long) in the groove. An important tendency in lamina cutting is for the basal tertiary segments to be slightly

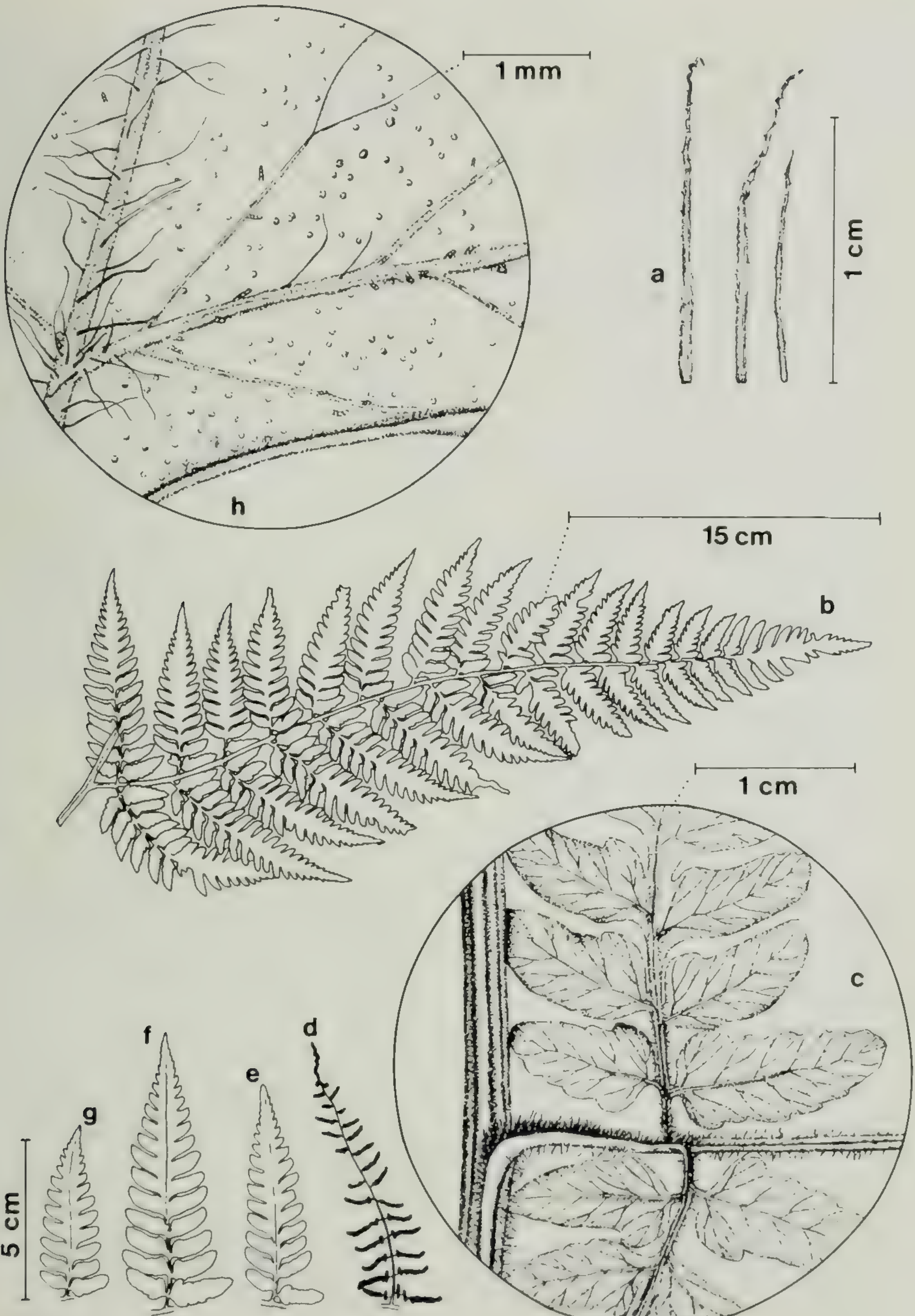

FIGURE 49. *Polybotrya cyathifolia* Fée. a. stem scales; b. basal pinna; c. rhachis-costa-costule junctures; d. fertile pinnule; e–g. sterile pinnules; h. abaxial view of lamina showing resinous glands. a,c,h: *L'Herminier s.n.* (P). b,g: *L'Herminier s.n.* (GH). d: collector unknown (GH). e,f: collector unknown (B).

gibbous at its base on both sides (Fig. 49c). This gives the pinnules a characteristic appearance, although it is somewhat difficult to describe. *Polybotrya osmundacea* rarely has these lobules and, if so, they are developed only on the acroscopic side. Most specimens of *P. cyathifolia* have the abaxial surface of the lamina covered with punctate, resinous glands (Fig. 49h); *P. osmundacea* rarely has such glands.

Specimens examined: GUADELOUPE. "near the house of Mr. Bovie," *L'Herminier s.n.* (P, GH, L, fragment NY).

MARTINIQUE. *Duss 1503* (NY, US), *3897* (NY), *4719* (F, US); *Hahn s.n.* (P); *Belanger s.n.* (F).

30. Polybotrya latisquamosa Moran, *sp. nov.* (Fig. 50, Map 19).

Polybotrya latisquamosa Moran, *sp. nov.* TYPE: Colombia. Meta: Cordillera La Macarena (extremo nordeste), macizo Renjifo, alrededores, alt. 1300–1900 m, 6–20 de enero 1951, *Idrobo & Schultes 1106* (holotype: US!; isotype: COL?).

Caulis 2 cm diam.; squamae castaneae, lineares vel anguste lanceolatae, 7–12 × 0.8–2.0 mm; petiolus ad basim squamatus, squamis castaneis, longioribus, 12–16 × 5–6 mm, deltatis vel late ovatis, marginibus pallidis erosis; lamina late deltata, 3-pinnata-pinnatifida, glabra in superficiebus utrinque, usque ad 13.5 × 5 cm, petiolulis usque ad 8 cm; segmenta tertiaria valde ascendentia basiscopice. Folia fertilia ignota.

Stem 2 cm thick, hemiepiphytic; *scales* castaneous, linear to narrowly lanceolate, ascending-spreading, darker and opaque in the center with lighter borders, margins erose, 7–12 × 0.8–2.0 mm. *Sterile leaves* up to 1.5 m (?); *petiole* scaly at the base with scales similar to those of the stem but much larger, 12–16 × 5–6 mm, deltate to broadly ovate; *lamina* broadly deltate (?), 3-pinnate-pinnatifid, glabrous on both surfaces; *pinnae* ca. 10–12 free pairs (?), alternate, the largest 45 × 26 cm; *pinnules* arranged anadromically, the proximal ones with stalks up to 8 mm long, the base strongly prolonged acroscopically, basiscopically shortened and strongly ascending, up to 13.5 × 5 cm; *tertiary segments* up to 3.5 × 1.3 cm, lanceolate, cuneate at the base, pinnatifid, 3–5 free below the pinnatifid apex, the basiscopic side strongly oblique, often with the first proximal 1–3 lobes completely suppressed; *costae* glabrous abaxially or with a few scattered, inconspicuous, less than 0.1 mm long, whitish, subulate hairs; *grooves* filled with reddish, inconspicuous hairs less than 0.1 mm long. *Fertile leaf* unknown.

The type location is a remote area in south-central Colombia, the Cordillera de Macarena, separated from the main Andean chain (Map 19). Since the holotype consists of only a portion of the stem and several incomplete pinnae, additional collections of this species would add greatly to the incomplete description.

Polybotrya latisquamosa resembles *P. osmundacea* because of its large decompound leaves with anadromically arranged pinnules but differs by its exceedingly large, broad, castaneous scales at the base of the petiole (Fig. 50d); thus the specific epithet. The stem scales differ from those of *P. osmundacea* by their deep castaneous color. The holotype is larger and more finely cut than the average *P. osmundacea* specimen, and the basiscopic sides of the pinnules and tertiary segments are extremely reduced and oblique-ascending (Fig. 50a). Finally, the major axes of *P. latisquamosa* are glabrous (Fig. 50e), unlike those of *P. osmundacea*, which are often pubescent.

31. Polybotrya sessilisora Moran, *sp. nov.* (Fig. 51, Map 20).

Polybotrya sessilisora Moran. TYPE: Colombia. Vaupés: Río Vaupés, Mitú y alrededores, 250 m, 8 September 1951, *Schultes & Cabrera 13963* (holotype: US!; isotypes: COL!, GH!).

Caulis hemiepiphyticus, 5–10 mm diam.; squamae appressae, ascendentes, lineares, 8–12 mm longae, atrocastaneae, marginibus pallidis et valde vehementer denticulatis; lamina usque ad 3-pinnata-pinnatifida, glabra, coriacea, pallide viridis; pinnae anguste deltatae vulgo 17–36 × 7–16 cm; pinnulae vulgo 3.5–10 × 1.2–3.0 cm, anadromicae, apicibus persaepe obtusis; rhachis et costae sparsim pubescentes, squamis fuscatis, appressis, flexuosis; venae conspicuae et prominulae. Folia fertilia usque ad 3-pinnata; lamina anguste alata viridis, marginibus leviter incrassatis; sori ca. 1 mm longi, discreti, circulares.

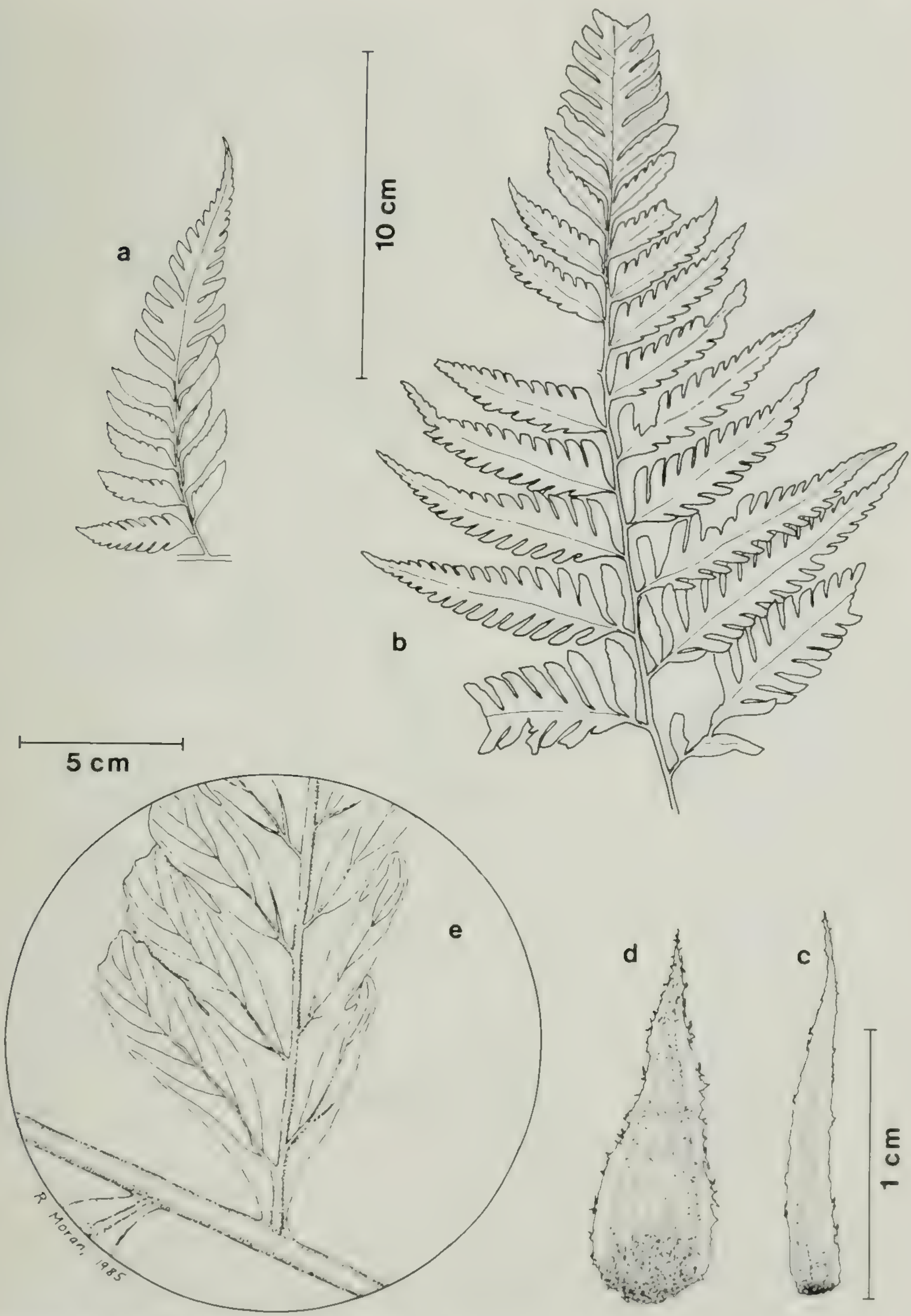

FIGURE 50. *Polybotrya latisquamosa* Moran. a. sterile pinnule; b. apex of sterile leaf; c. stem scale; d. scale from petiole base; e. pinnule from medial pinna. a–e: *Idrobo & Schultes 1106* (US).

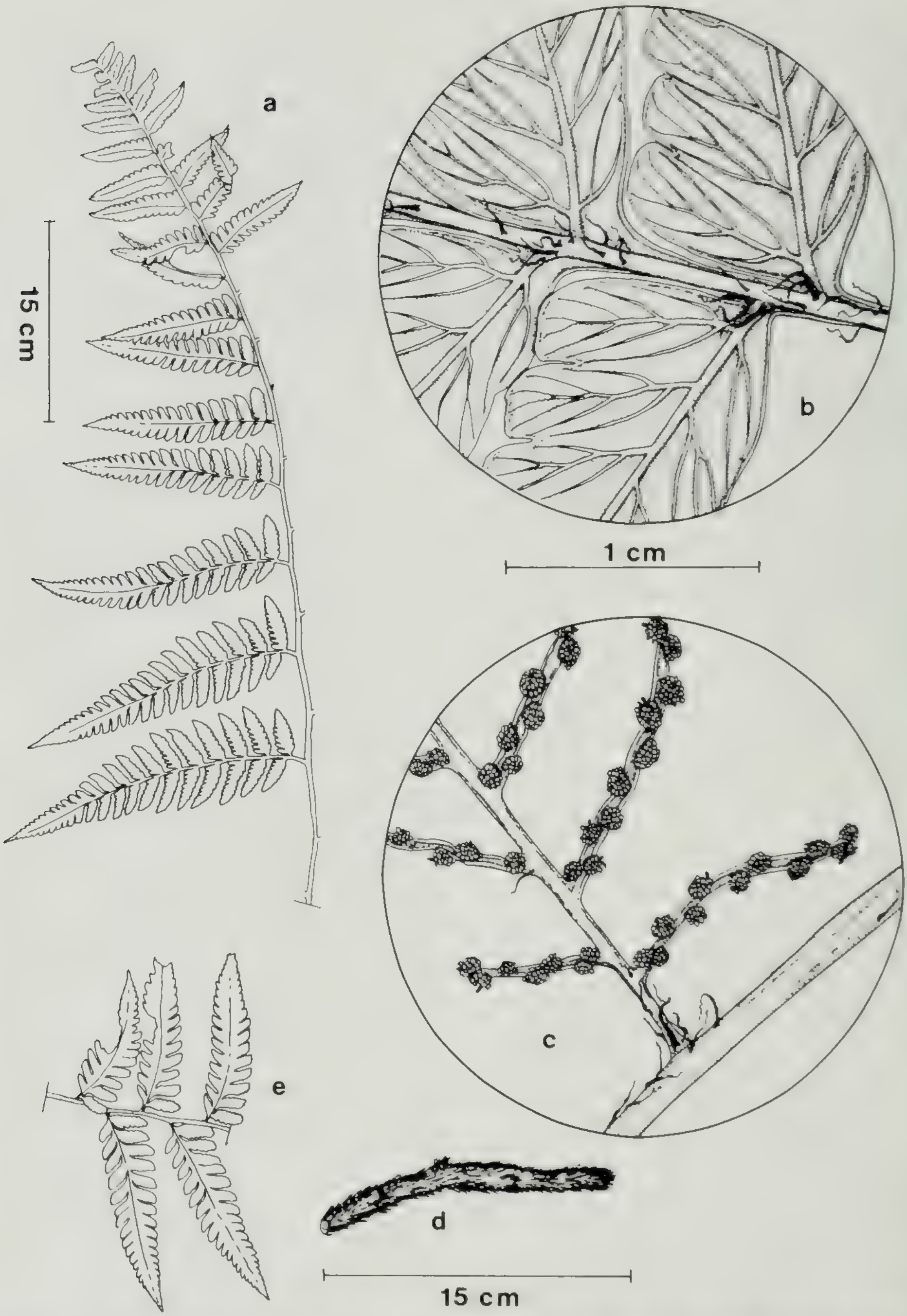

FIGURE 51. *Polybotrya sessilisora* Moran. a. distal half of sterile leaf; b. abaxial surface of costa and pinnules (note the thickened, lighter colored margin and dark tortuous scales); c. fertile pinnule, abaxial view (note the thickened margins and discrete sori); d. stem showing straight, appressed scales; e. medial pinnules of basal pinna, acroscopic side is up. a,c,d,e: *Schultes & Cabrera 13963* (COL). b: *Prance et al. 15332* (NY).

Stems 5–10 mm thick, hemiepiphytic; *scales* appressed, ascending, linear, 8–12 mm long, dark castaneous with lighter narrow borders and strongly denticulate margins. *Sterile leaves* up to 75 cm long; *petiole* ½ to as long as the lamina, scaly with scales similar to those of the stem, but more tortuous and spreading, the base mostly cordate; *lamina* to 40 cm long, up to 3-pinnate-pinnatifid, narrowly deltate, the tissue glabrous, coriaceous, light green, the margins glabrous; *pinnae* narrowly deltate, 17–36 × 7–16 cm, the proximal acroscopic pinnule or segment slightly prolonged above the rest; *pinnules* to 3.5–10 × 1.2–3 cm, arranged anadromically, the basiscopic margin thickened and decurrent on the costa, the apex of the less cut medial pinnules merely acute or obtuse; *veins* conspicuous and prominulous abaxially; *axes* moderately to sparsely pubescent abaxially, the hairs colorless, tawny, 0.5–1.0 mm long; *grooves* of axes decurrent on those of lower order, not interrupted, pubescent within by tiny, less than 0.2 mm long, reddish, jointed hairs, covered with dark, spreading, tortuous, denticulate scales like those of the petiole. *Fertile leaves* 3-pinnate, botryoid, the margins slightly thickened; *sori* sessile, round, about 1 mm long; *spores* (44)46–52(56) microns long.

Polybotrya sessilisora grows in lowland forests of the northern Amazon basin (Map 20). It is probably more common than the number of collections suggests, since the northern Amazon basin is poorly collected. I suspect that this species also occurs in the adjacent Guiana Highlands.

The specific epithet refers to the botryoid sori that are sessile instead of short-stalked as in other species of *Polybotrya*. Moreover, the sori are embedded in the lamina, which is not completely reduced to the axis (Fig. 51c). As evidenced by outgroup comparison to other dryopteroid ferns, the ancestor to *Polybotrya* surely had fertile leaves with discrete, round sori from which the lamina was reduced. Because the lamina of *P. sessilisora* is not fully reduced, I interpret its fertile leaf as the most primitive in the genus. No other species in the genus has this distinct kind of fertile leaf.

Another distinctive feature of *P. sessilisora* is the dark castaneous scales that contrast sharply with the light green lamina. The scales of the axes are spreading and tortuous, whereas those of the stem are appressed and straighter (Fig. 51b,d). These scales become smaller and narrower in the distal parts of the lamina until they become uniseriate, appressed hairs. The lamina is always broadest at the base, in contrast to the closely related *P. osmundacea*, which is usually reduced at the base. *Polybotrya osmundacea* also tends to be much more highly dissected when leaves of equal size are compared.

Specimens examined: COLOMBIA. **Vaupés:** Río Vaupés, Mitú y alrededores, 250 m, *Schultes & Cabrera 13963* (COL, GH, US).

BRAZIL. **Amazonas:** Tapuruquara, beside road to airport, *Prance et al. 15332* (NY); Reserva Experimental, km 60, Manaus–Caracarai road, *Conant 1016* (GH), *1482* (GH); Reserva Ducke, km 26, Manaus–Itacoatiara road, *Conant 1080* (GH).

BRAZIL–GUYANA BOUNDARY: Akarai Mountains, height of land between drainage of Río Mapuera (Trombetas tributary) and Shodikar Creek (Essequibo tributary), dense forest 600–800 m, *A.C. Smith 2984* (GH, NY).

32. **Polybotrya canaliculata** Klotzsch (Fig. 52, Map 19).

Polybotrya canaliculata Klotzsch, Linnaea 20:429. 1847. LECTOTYPE: Venezuela. Aragua: Colonia Tovar, 1846, *Moritz 278* (lectotype: B!; isolectotypes: F!, GH!, L!, NY!, P!, US!; photo GH! of L). LECTOPARATYPE: Colonia Tovar, 1846, *Karsten (Coll. II) no. 13* (B!; isolectoparatypes; BM!, L!; photo of L specimen, NY!).

Acrostichum canaliculatum (Klotzsch) Hooker, Species Filicum 5:247. 1864.

Stems 0.5–2 cm thick, hemiepiphytic; *scales* ascending with spreading tips, 12–20 × 0.7–1.2 mm, dull brown to dark purple brown, concolorous or rarely with a very narrow hyaline border, the margins entire to denticulate, opaque to slightly thickened at the center and base. *Sterile leaves* up to 1.8 m long; *petiole* up to 45 cm long, shorter than the lamina, scaly at the base or throughout, the scales becoming progressively smaller and more ovate-lanceolate and erose-denticulate upwards, with a blackened basal point of attachment; *lamina* glabrous, lanceolate to triangular or subtriangular, 50–80 cm wide, to (4)3-pinnate-pinnatifid, subcoriaceous, the abaxial surface lighter in color than the adaxial; *basal*

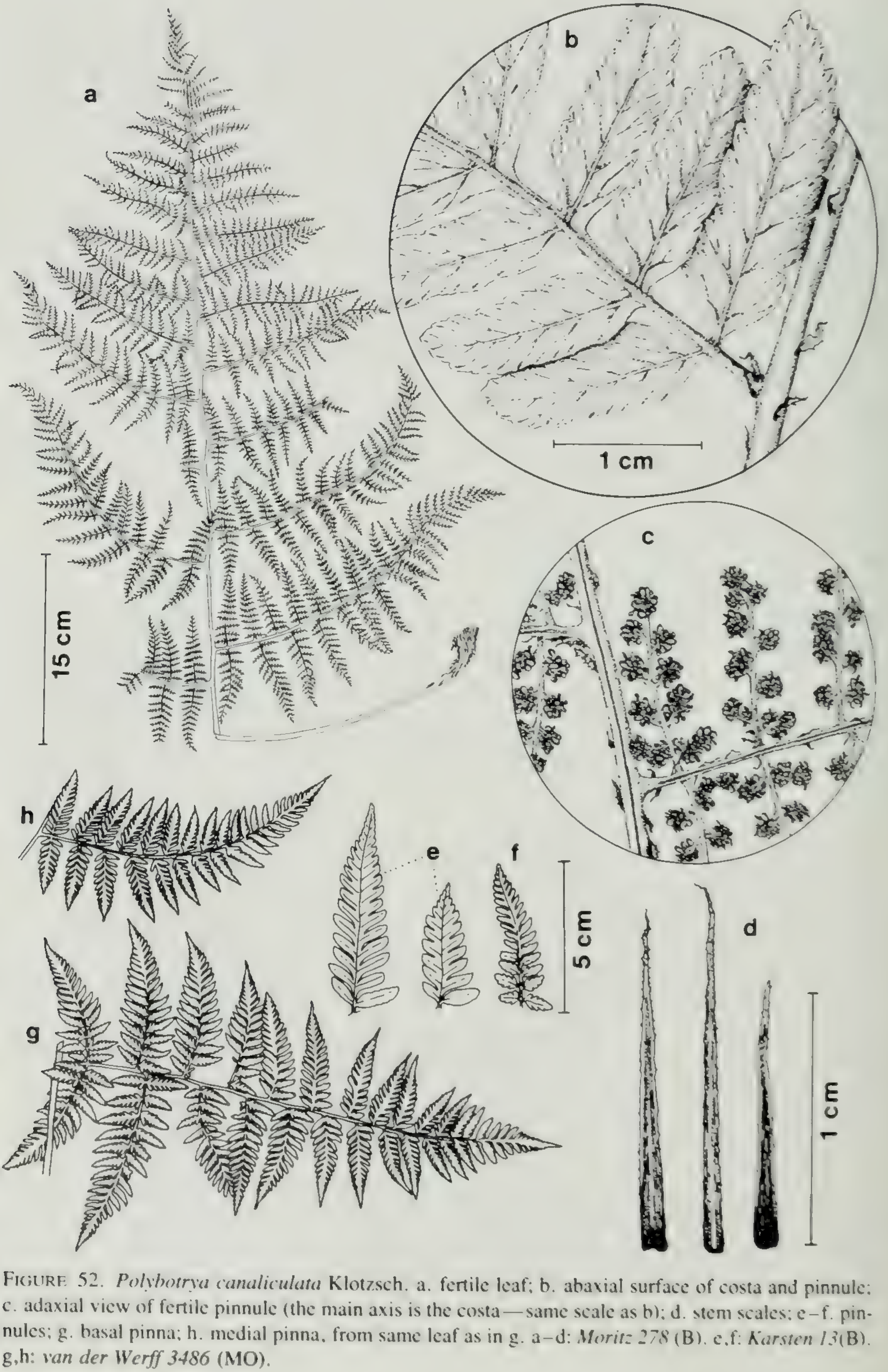

FIGURE 52. *Polybotrya canaliculata* Klotzsch. a. fertile leaf; b. abaxial surface of costa and pinnule; c. adaxial view of fertile pinnule (the main axis is the costa—same scale as b); d. stem scales; e–f. pinnules; g. basal pinna; h. medial pinna, from same leaf as in g. a–d: *Moritz 278* (B). e,f: *Karsten 13*(B). g,h: *van der Werff 3486* (MO).

pinnae triangular to subtriangular, up to 40 × 28 cm, the lowermost pinnate throughout except pinnatifid at the extreme apex; *pinnules* arranged catadromically or anadromically, up to 16 × 6.5 cm, triangular-lanceolate, the acroscopic side usually prolonged; *costules* adaxially deeply grooved and bordered by a raised, erect to spreading flap of tissue; *tertiary segments* entire to pinnatifid (deeply so in large leaves), equilateral at the base with a rounded to acute apex; *axes* scaly, the scales scattered, flaccid, membranaceous, ovate to lanceolate, denticulate, 1–3.5 mm long, the abaxial surface usually glabrous; *grooves* pubescent within, and especially at segment junctures, the hairs tiny, less than 0.2 mm long, reddish. *Fertile leaves* botryoid, 0.8 × 0.6 m, 4-pinnate; *axes* with numerous septate hairs that often grade into narrow scales; *pinnae* up to 30 cm long, subtriangular; *sori* round to obovate, distinctly stalked, the stalk about 1 mm long; *spores* (50)55–66(70) microns long.

This species grows in cloud forests in the Andes of northern Venezuela from 1200 to 1600 m (Map 19). Van der Werff and Smith (1980) state that this species can be abundant locally, but that the plants rarely bear fertile leaves.

The specific epithet refers to the raised flap of tissue that borders the costules and accentuates the depth of the central groove. This character is not diagnostic, since other decompound *Polybotrya* species also have raised costular ridges, although in *P. canaliculata* these ridges tend to be relatively taller and more well developed.

When available, the botryoid fertile leaves (Fig. 52a,c) distinguish this species from *P. osmundacea* and its allies. Distinguishing vegetative characters are the dull brown, concolorous stem scales, and the major axes with prominent, ovate to lanceolate, flaccid scales (Fig. 52b). The pinnule arrangement of *P. canaliculata* may be either anadromic or catadromic. This variation is peculiar because the pinnule arrangement is usually constant within most species of *Polybotrya*. A similarly variable species in this respect is *P. gomezii*, an endemic from Costa Rica. I interpret *P. canaliculata* as a primitive species of *Polybotrya* because of its decompound lamina and botryoid fertile leaf.

I have chosen the Moritz collection as the lectotype because of its wide distribution in herbaria and the excellent quality of the specimens.

Specimens examined: VENEZUELA. **Aragua**: Colonia Tovar, 1846, *Moritz 278* (B, BM, F, GH, L, NY, P, US); Colonia Tovar, 1846, *Karsten 13* (B, BM, L; photo of L specimen, NY); Parque Nacional Henri Pittier, bosque de Rancho Grande, *Tschudi 166* (VEN); Colonia Tovar, 1854–5, *Fendler 262* (GH, MO, NY, P, PH, US). **Falcón:** Sierra de San Luis, arriba de Sta. María, alt. 1200 m, 5 June 1979, *van der Werff 3486* (MO, UC); Sierra de San Luis, selva nublada, entre La Chapa y Uria, *Steyermark 99185* (VEN). **Yaracuy:** Dtto. Bolívar, entre las Parchitas, Tierra Fria y Ojo de Agua, *Ortega & Smith 2498* (PORT), *2511* (PORT). **State unknown**: Andes of Venezuela, 1889, *Goebel s.n.* (P).

33. Polybotrya semipinnata Fée (Fig. 53, Map 18).

Polybotrya semipinnata Fée, Crypt. Vasc. Brésil. 1:16. 1869. TYPE: Brazil. Rio de Janeiro: Yacuacanga, 15 June 1869, *Glaziou 2427* (K, P!, RB!, US!; photo of K specimen at US!).

Aspidium scandens Raddi, Plant. Brasil. 1:34, tab. 49. 1825. TYPE: Brazil. *Raddi s.n.* (FI; isotype: K, photo GH!).

Polybotrya scandens (Raddi) Christ, Bull. Herb. Boissier, II. 4:965. 1904. *nom. illegit.*, *non* Fée 1852.

Stem 1–1.5 cm thick, hemiepiphytic; *scales* membranous, spreading, mostly 9–12 × 0.5–1.2 mm, bright castaneous, concolorous or with a dark central stripe and lighter borders, the margins denticulate to strongly erose. *Sterile leaves* up to 1 m long; *petiole* ⅓ to ½ the length of the lamina; *lamina* ovate to lanceolate to 3-pinnate but mostly 2-pinnate-pinnatifid throughout, generally 45–60(75) × 30–55(64) cm, coriaceous, glabrous except on major axes; *pinnae* broadly triangular to ovate, mostly 15–30 × 11–17 cm, divided at base and soon becoming pinnatifid distally; *pinnules* 5–10(13) × 2–3 cm, lanceolate, anadromic throughout, the bases mostly cuneate, unequal, the basiscopic side more narrowly cuneate and the acroscopic side slightly prolonged, proximal ones with a 3–5 mm long stalk, rarely with the lowermost acroscopic segment cut to the costule; *axes* pubescent abaxially with hairs less than 0.1 mm long, stiff, colorless, subulate, the scales few or absent; *grooves* glabrous or nearly so within, decurrent on those of the next lower order. *Fertile leaves* smaller than the sterile, 3-pinnate (-pinnatifid), coenosoric; *tertiary segments* oblong, generally 3–7 mm long; *sporangial stalk* paraphysate; *spores* (48)50–62(66) microns long.

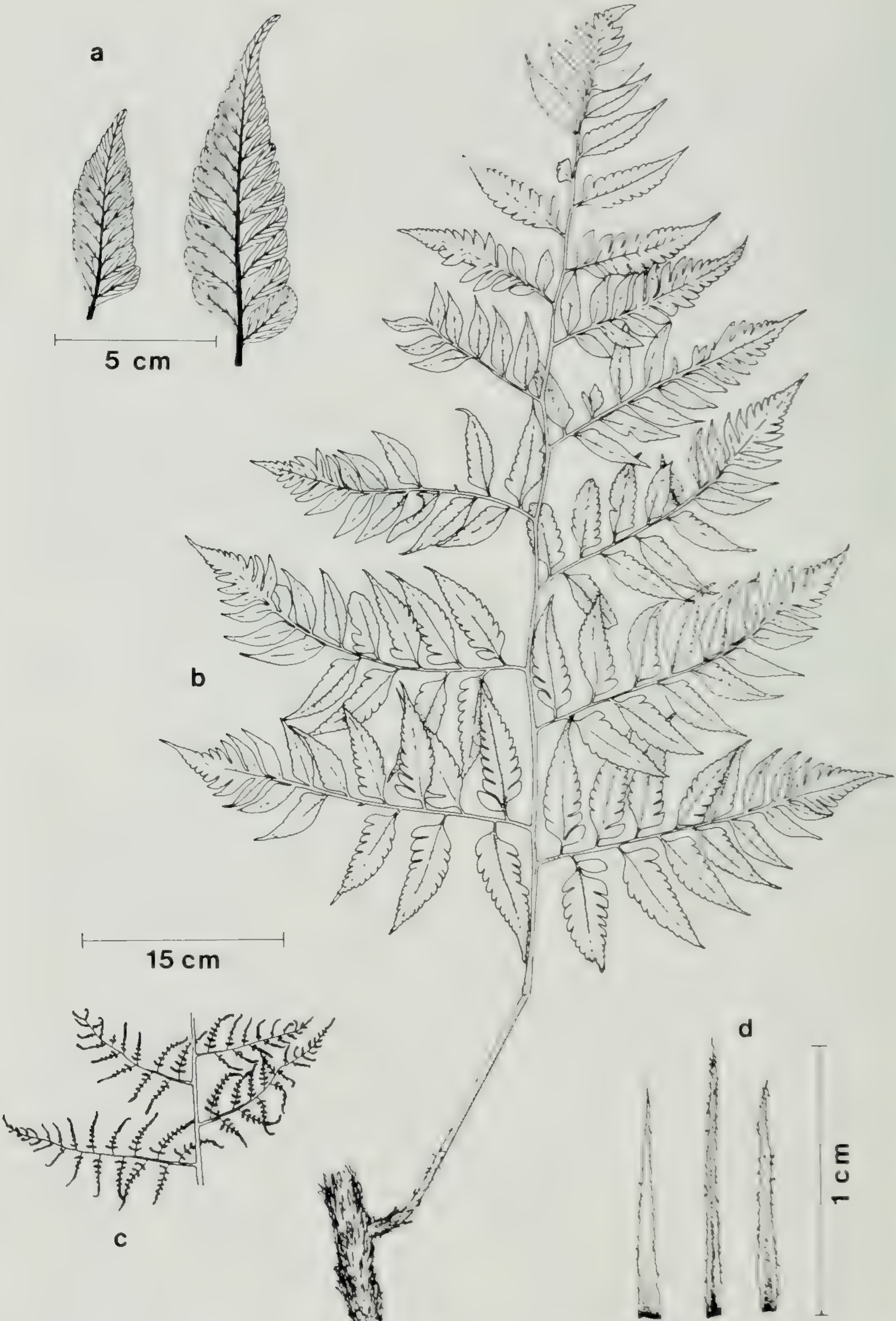

FIGURE 53. *Polybotrya semipinnata* Fée. a. sterile pinnules; b. sterile leaf; c. middle pinnae of fertile leaf; d. stem scales. a–c: *Brade 8061* (PH). d: *Duarte et al. 65322* (F).

Other illustrations: Raddi, Plant. Brasil. tab. 49. 1825; Mettenius, Filices Hort. Lips., 23, tab. 2, figs. 1–6. 1856 (as *P. acuminata*); Brade, Bradea 1:64, fig. 1; 67, fig. 9. 1971 (as *P. scandens*).

Polybotrya semipinnata is one of five *Polybotrya* species that are endemic to the coastal mountains of southeastern Brazil (Map 18, Table 2), a distribution that emphasizes the biogeographic distinctness of the Serra do Mar Mountains. The altitudinal range of *P. semipinnata* is from 800 to 1000 m.

This plant, easily recognized by its lamina cutting, is not readily confused with other species of *Polybotrya*. The pinnule bases are distinctive because they are stalked and more narrowly cuneate on the basiscopic side. The pinnae are stouter and much less divided compared to those of other decompound *Polybotrya* species; the distal portions soon become pinnatifid, a characteristic that accentuates this less-cut appearance.

An earlier published name, *P. acuminata* Link, has often been applied to this species. Since the type specimen cannot be located and I cannot discern from Link's description the species he had in mind, I treat *P. acuminata* as a name of uncertain application.

Specimens examined: BRAZIL. **Rio De Janeiro:** Yacuacanga, *Glaziou 2427* (P, RB, US; photo of K specimen at US); Estrada Velha da Bocaina, Teresópolis, *Duarte et al. 65322* (F, LP); Serra dos Orgãos, Teresópolis can. Quebrafrasco, 1000 m, *Brade 16456* (RB). **São Paulo:** Piruhyba, *Loefgren & Duvall 36217* (RB); prope Rio Grande ad São Paulo Railway, 800 m, *Wettstein & Schiffner s.n.* (P); Alto da Serra, *Luederwaldt s.n.* (BM, NY), *21547* (NY); Iguape, morro das Pedras, Serrinha Peroupara, *Brade 8061* (NY, PH, UC, US); Pilar, *Gerdes 102* (NY, UC). **Sta. Catarina:** without locality, *Schwacke s.n.* (P).

34. Polybotrya speciosa Schott (Fig. 54, Map 21).

Polybotrya speciosa Schott, Genera Filicum tab. 7. 1834. NEOTYPE: (here chosen) Schott, Genera Filicum tab. 7, based on material from "Brasiliae provincia Sebastianopolitana."

Polybotrya tomentosa Brade, Arq. Inst. Biol. Veg. Rio de Janeiro 1:224, fig. 2, plates 2 and 3. 1935. TYPE: Brazil. Minas Gerais: Serra do Itatiaia Maromba, 25 June 1930, *Brade 10351* (holotype: RB!).

Polybotrya osmundacea Willd. var. *crispopaleacea* Rosenst., Feddes Repert. 21:349. 1925. TYPE: Brazil. São Paulo: Alto da Serra, 11 February 1925, *Brade 5838* (S; isotype: UC!).

Polybotrya litoralis Brade, Bradea 1:26, tab. 1, fig. 2. 1969. TYPE: Brazil. Rio de Janeiro: Angra dos Reis, Serra do Mar, 29 June 1935, *Brade 14943* (holotype: RB!).

Polybotrya rosenstockiana Brade, Bradea 1:27, tab. 1, fig. 3. 1969. TYPE: Brazil. Rio de Janeiro: Serra dos Orgãos, Corrego Beija-flor, *Brade 16579* (holotype: RB!; isotype: LP!).

Stem 1–3 cm thick; *scales* commonly brick red, rarely dull brown, concolorous or with a dark central stripe, generally 8–20(27) × 0.5–1.5(2.0) mm, spreading, membranous, the margins denticulate to strongly erose. *Sterile leaves* up to 1.4 m long; *petiole* 1/10–1/4 the length of the lamina; *lamina* to 1.2 × 0.8 m, lanceolate to ovate, to 3-pinnate but mostly 2-pinnate-pinnatifid throughout, tomentose to glabrous, the margins sparsely ciliate to glabrous; *pinnae* to 40 × 15 cm, free pinnules usually 5–9; *pinnules* acroscopic, short to long triangular, mostly 4.5–8.0(10.0) × 1.5–3.5 cm, the base stalked, the stalk 2–4 mm long, the acroscopic side prolonged, the basiscopic side oblique; *tertiary segments* generally oblong, the margins entire to crenulate or dentate; *axes* tomentose to glabrous or subglabrous, the hairs usually 0.1–0.5 mm long, the scales few, appressed, tortuous, narrow; *grooves* pubescent within, the hairs reddish. *Fertile leaves* coenosoric, 3-pinnate; *sporangial stalks* paraphysate; *receptacle* glabrous or with multicellular, branched paraphyses, these as long as or slightly longer than the sporangia; *spores* (56)60–75(82) microns long.

Other illustrations: See original descriptions cited above; Brade, Bradea, tab. 3, fig. 4 (as *P. littoralis*); tab. 4, fig. 1 (as *P. rosenstockiana*); tab. 4, fig. 3; tab. 6, figs. 12, 13 & 15. 1971.

Polybotrya speciosa is endemic to the Serra do Mar Mountains along the coast of southeastern Brazil (Map 21). It differs from the four other species of *Polybotrya* there by its combination of strongly denticulate, red stem scales, finely cut lamina, and multicellular, branched paraphyses (Fig. 54). The pubescence of the abaxial surface varies from densely tomentose to nearly glabrous.

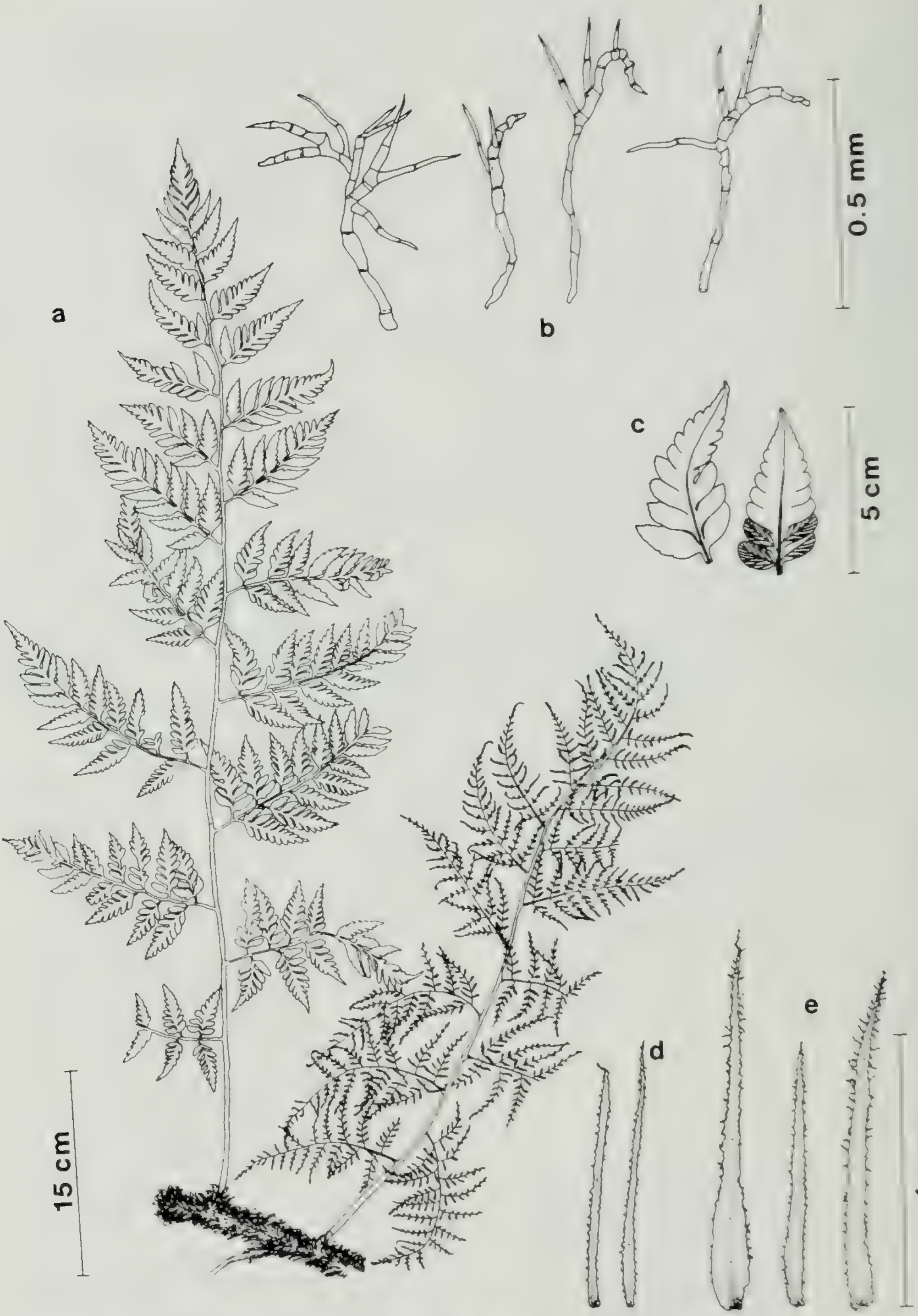

FIGURE 54. *Polybotrya speciosa* Schott. a. sterile and fertile leaves; b. branched paraphyses; c. pinnules; d,e. stem scales. a,b,e: *Brade 16579* (RB). c,d: *Brade 10351* (RB).

Five of the specimens examined had the adaxial surface slightly pubescent whereas the remaining were completely glabrous. No other species of *Polybotrya*, except *P. pilosa*, has branched paraphyses.

The spore size varies greatly, perhaps reflecting different ploidy levels. The averages from eight collections, with 15 spores measured from each, are as follows (in microns): 56, 57, 57, 58, 69, 69, 79, 82. This problem needs further study of additional collections and cytological samples.

I have been unable to locate Schott's type, but I feel quite certain that Schott's excellent plate represents this species. Schott's specimens became part of the Cardinal Hynald herbarium now located in Budapest, Hungary (BP). The curator of the fern collection at Budapest, Mr. Tibor Szerdahelyi, informed me (in litt.) that much of Schott's type material had been destroyed during World War II and that he could not find the type.

My placement of the three species described by Brade in synonymy with *P. speciosa* requires comment. I find no differences between the types of *P. tomentosa* and *P. litoralis*—the two might well have been collected from the same individual. Given this likeness, I find it odd that Brade (1969c) did not mention *P. tomentosa* in his discussion after the description of *P. litoralis*. I also place *P. rosenstockiana* and *P. osmundacea* var. *crispopaleacea* in synonymy, although they differ slightly from most specimens of *P. speciosa* by their somewhat broader stem scales (Fig. 54, compare d & e). They also differ by their leaves, which are less pubescent, primarily so along the axes and veins. Both these characters, however, intergrade and do not correlate with any others.

Specimens examined: BRAZIL. **Rio de Janeiro:** Serra dos Orgãos, Corrego Beijaflor, *Brade 16579* (LP, RB); Serra do Taquaral, *Brade 17464* (MO, NY); Therezopolis, *Brade 9773* (BM, UC), *9843* (NY); Parque Nacional de Serra dos Orgãos, *de la Sota 2343* (LP); Serra dos Orgãos, Morro Assu, *Luetzelburg 6858* (US); Organ Mts., *Rose & Russell 20790* (US); Corcavado, collected by the U.S. South Pacific Exploring Expedition, 1838–42 (NY, US); Mt. Tijuca, *Cuyler 4796* (US); Angra dos Reis, Serra do Mar, *Brade 14943* (RB); Guanabara, Estrada do Sumaro, *Pabst et al. 6772* (LP). **Minas Gerais:** Serra do Itatiaia, Maromba, *Brade 10351* (RB); Itatiaia, Maromba, *Brade 20214* (F, LP, MO, NY); same locality, *Brade 12616* (BM); Tijuca, *Alston 8991* (BM). **São Paulo:** Alto da Serra, *Brade 5838* (UC). **State unknown:** "Brazil," *Webb 26* (GH).

35. Polybotrya pilosa Brade (Fig. 55, Map 20).

Polybotrya pilosa Brade, Bradea 1:27, tab. 1, fig. 4. 1969. TYPE: Brazil. Rio de Janeiro: Teresópolis, Varesea, 1000 m, 27 October 1929, *Brade 9787* (holotype: RB!; isotypes: NY!, UC!).

Differing from *P. tomentosa* only by characteristics of the pubescence; *hairs* 1–2(2.5) mm long, pilose, acicular, pluricellular, whitish or tawny, disposed along the abaxial surface of the veins and major axes, rarely on the intervening laminar tissue between the veins, also occurring on the adaxial surface and protruding from the costal and rhachidial grooves. Paraphyses present, of both branched and unbranched types.

Polybotrya pilosa is endemic to southeastern Brazil (Map 20). This species may be subject to reinterpretation in the future, as it differs from *P. speciosa* only by its pubescence, which shows no intergradation between the two species. The hairs of *P. speciosa* are less than 1 mm long, somewhat tortuous, and occur on the veins and intervening laminar tissue. The hairs of *P. pilosa* are more than 1 mm long, straightish, and acicular; they occur only along the veins, *not* on the intervening laminar tissue (Fig. 55a). These differences are readily apparent to the unaided eye. The reinterpretation of *P. pilosa* will require fieldwork designed to study intra- and interpopulational variation in southeastern Brazil.

Other illustrations: See Brade's original description, cited above.

Specimens examined: BRAZIL. **Rio de Janeiro:** "near Rio de Janeiro," collected by U.S. Exploring Expedition, 1838–42 (US); Tijuca, *Brade 20733* (NY, UC); "Rio Janeiro," 1851, *Andersjon s.n.* (LP); Organ Mts., *Wagner s.n.* (GH); Teresópolis, Varesea, *Brade 9787* (NY, RB, UC); Serra Estrela, *Weddell 952* (P); "Brasilia," *Riedel 81* (GH).

FIGURE 55. *Polybotrya pilosa* Brade. a. costa and pinnule with characteristic long, acicular hairs; b. sterile leaf; c. stem scales. a: *Wagner s.n.* (GH). b,c: *Brade 9787* (RB).

Names of Uncertain Application

Polybotrya acuminata Link, Hort. Berol. 2:135. 1833. *Psomiocarpa acuminata* (Link) Presl, Epim. Bot. 162. 1849. TYPE: Brazil. Collector? I have been unable to locate the type and cannot discern from the original description the taxon to which this name applies. The type specimen may have been lost during World War II; I have, however, Link's other type specimens from Berlin. Mettenius (1856, tab. 2) has an excellent illustration of *P. semipinnata*, which he refers to as *P. acuminata*, but I do not know whether he saw type material.

Polybotrya fulvostrigosa Christ, Bull. Herb. Boissier, II. 1:70. 1901. TYPE: Peru. Loreto: Cerro de Canchahuaya, *Huber 1448*. I cannot find the type and am uncertain from Christ's description to what species this name belongs.

Polybotrya lomarioides Mettenius, Filices Lechler. 2:5. 1858. TYPE: Peru. Puno: San Gaván, *Lechler s.n.*. I have not seen the type and cannot be certain from the description if this name applies to a *Polybotrya* species or to another genus.

Polybotrya nutans Kunze, Linnaea 9:24. 1834. TYPE: Peru. "Sylvae flor. Peruv. ad Pampayaco in cortice arborum vetustarum parasitica, Jul. 1829," *Poeppig s.n.* (B!, P!). The fertile leaf of the type specimen came from a species of *Polybotrya*, but I do not know which one. The sterile leaf of the type specimen is a tree fern, perhaps a species of *Trichipteris*.

Polybotrya scandens Fée, Genera Filicum 47. 1852. TYPE: Venezuela. Lagunetta, *Galeotti*. I have not seen the type and cannot ascertain from Fée's description the species to which this name applies. I suspect it is *P. osmundacea*. Windisch (1982) reported Fée's specimen of *P. scandens* to be at the Botanical Gardens in Rio de Janeiro (RB). Although I received other Fée specimens from RB, *P. scandens* was not among them. Fée gives the location as "Lagunetta, Mexico," but this site is certainly an error; see the discussion under *P. serratifolia*.

Polybotrya trapezoides Link, Filicum Species 164. 1841. TYPE: Cultivated plant at Berlin of unknown origin (B!). I received a specimen from Berlin (B) labelled as species but cannot be sure that this is the type. This specimen, however, is certainly not a species of *Polybotrya*. Because it is so young, I am uncertain what genus it represents.

Excluded Taxa

Excluded Subgenera

Polybotrya subg. *Ectoneura* Fée, Mém. Fam. Foug. (Hist. Acrost.) 75. 1845 (*nomen illegit.*). = *Bolbitis* (*fide* Hennipman 1977).

Polybotrya subg. *Egenolfia* Fée, Mém. Fam. Foug. (Hist. Acrost.) 14. 1845. = *Bolbitis* (*fide* Hennipman 1977).

Excluded Sections

Polybotrya sect. *Arthrobotrya* v.A.v.R., Handb. 725. 1908. = *Lomariopsis* sect. *Polyseriatae* (*fide* Holttum 1978).

Polybotrya sect. *Egenolfia* Diels, E&P Nat. Pfl. Fam. 1:195. 1900. = *Bolbitis* (*fide* Hennipman 1977).

Polybotrya sect. *Lomagramma* Kuhn, Ann. Mus. Bot. Ludg.-Bat. 4:198. 1899. = *Lomagramma* (*fide* Holttum 1978).

Polybotrya sect. *Teratophyllum* Christ, Farnkr. Erde 42. 1897. = *Lomariopsis* sect. *Polyseriatae* (*fide* Holttum 1978).

Excluded Species

Polybotrya acrostichoides Kuhn, Fil. Afr. 52. 1868. = *Bolbitis acrostichoides* (Sw.) Ching (*fide* Hennipman 1977).

Polybotrya apiifolia Kunze, Farnkr. 1:142, tab. 62. 1844. = *Psomiocarpa apiifolia* (Kunze) Presl.

Polybotrya appendiculata (Willd.) J. Smith, Jour. Bot. 4:150. 1841. = *Bolbitis appendiculata* (Willd.) Iwatsuki, (*fide* Hennipman 1977).

Polybotrya arfakensis Gibbs, Arfak 71. 1917. = *Alsophila biformis* Rosenstock (*fide* Holttum 1963).

Polybotrya articulata Fée, Mém. Fam. Foug. (Hist. Acrost.) 74, tab. 37. 1845. = *Teratophyllum articulatum* (Fée) Kuhn (*fide* Holttum 1978).

Polybotrya aspidioides Grisebach, Cat. Pl. Cub. 276. 1866. = *Atalopteris aspidioides* (Grisebach) Maxon & C. Chr.

Polybotrya asplenifolia (Belanger) Presl, Tent. Pterid. 231. 1836. = *Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya aurita Blume, Fl. Jav. Fil. 15, tab. 1. 1828. = *Stenosemia aurita* (Sw.) Presl (*fide* Christensen 1905).

Polybotrya bifurcata (L.f.) J. Smith, Jour. Bot. 4:150. 1841. = *Elaphoglossum bifurcatum* (Jacq.) Mickel (*fide* Mickel 1980).

Polybotrya blumeana (Fée) Mettenius, Fil. Lips. 24, tab. 2, fig. 10. 1856. = *Leptochilus lomarioides* Blume.

Polybotrya cervina (L.) Kaulf., Enum. Fil. 55. 1824. = *Olfersia cervina* (L.) Kunze, Flora 7:312. 1824.

Polybotrya cicutaria Blume, Enum. Fil. 100. 1828. = *Stenosemia aurita* (Sw.) Presl (*fide* Christensen 1905).

Polybotrya duplicato-serrata Hayata, Ic. Fl. Formosa 5:305, fig. 123. 1915. = *Bolbitis rhizophylla* (Kaulf.) Hennipman (*fide* Hennipman 1977).

Polybotrya exaltata Brackenridge, U.S. Expl. Exp. 16:78. 1854. = *Bolbitis rhizophylla* (Kaulf.) Hennipman (*fide* Hennipman 1977).

Polybotrya filiculifolia (L.) Farw., Amer. Midl. Nat. 12:303. 1931. = *Anemia?*

Polybotrya flabellata (Willd.) Mettenius, Ann. Sci. Nat., Paris, V, 2:206. 1864. = *Peltapteris peltata* (Sw.) Morton.

Polybotrya fraxinifolia (Presl) Mettenius, Fil. Lechler. 2:8. 1959. = *Bolbitis serratifolius* (Kaulf.) Schott (*fide* Hennipman 1977).

Polybotrya furcata (L.f.) Kuhn, Fil. Afr. 52. 1868. = *Elaphoglossum bifurcata* (Jacq.) Mickel (*fide* Mickel 1980).

Polybotrya gaudichaudiana (Gaudich.) Moore, Index Fil. XV. 1857. = *Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya hamiltoniana (Wallich) Fée, Mém. Fam. Foug. (Hist. Acrost.) 78. 1845. = *Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya helferiana Kunze, Farnkr. Erde 2:35, tab. 94. 1848. = *Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya intermedia Fée, Mém. Fam. Foug. (Hist. Acrost.) 76, tab. 40, fig. 1. 1845. = *Bolbitis rhizophylla* (Kaulf.) Hennipman (*fide* Hennipman 1977).

Polybotrya lomarioides (Blume) Kuhn, Ann. Mus. Ludg.-Bat. 4:295. 1869. = *Lomagramma lomarioides* (Blume) J. Smith (*fide* Holttum 1978).

Polybotrya marattioides Brackenridge, U.S. Expl. Exped. 16:79. 1854. =*Asplenium marattioides* (Brackenridge) C. Chr. (*fide* Christensen 1905).

Polybotrya marginata Blume, Enum. Pl. Jav. 100. 1828. =*Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya montana (Gaudich.) Moore, Index Fil. 350. 1862. =*Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya nana Fée, Mém. Fam. Foug. (Hist. Acrost.) 75, tab. 38, fig. 1. 1845. =*Blechnum lanceolatum* (R. Br.) Sturm. (*fide* Christensen 1905).

Polybotrya neglecta Fée, Mém. Fam. Foug. (Hist. Acrost.) 75, tab. 39, fig. 2. 1845. =*Bolbitis rhizophylla* (Kaulf.) Hennipman (*fide* Hennipman 1977).

Polybotrya nieuwenhuisenii Raciborski, Bull. Int. Ac. Cracovie 57. 1902. =*Heterogonium stenosemioides* (Baker) Christ (*fide* Holttum 1975).

Polybotrya nodiflora Belanger, Voy. Ind. Or. Bot. 2:17. 1833. =*Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya orientalis Blume, Enum. Pl. Jav. 99. 1828. =*Stenosemia aurita* (Sw.) Presl (*fide* Christensen 1905).

Polybotrya peltata (Sw.) J. Smith, Jour. Bot. 4:150. 1841. =*Peltapteris peltata* (Sw.) Morton.

Polybotrya plumieri (Fée) Moore, Index Fil. 13. 1857. =*Elaphoglossum plumieri* Moore (*fide* Proctor 1977).

Polybotrya polyphylla (Brackenridge) C. Chr., Index Fil. 505. 1906. =*Lomagramma polyphylla* Brackenridge.

Polybotrya prolifera Mettenius, Fil. Lips. 24, pl. 2, fig. 11. 1856. =*Bolbitis subcrenata* (Hooker & Grev.) Ching (*fide* Hennipman 1977).

Polybotrya pteroides (J. Smith) Kuhn, Ann. Mus. Bot. Lugd.-Bat. 4:295. 1869. =*Lomagramma pteroides* J. Smith (*fide* Holttum 1978).

Polybotrya quercifolia (Retz.) Mettenius, Fil. Lechler. 2:12. 1859. =*Leptochilus zeylandicus* (Houtt.) C. Chr. (*fide* Christensen, 1905).

Polybotrya rhizophylla (Kaulf.) Presl, Tent. Pterid. 231. 1836. =*Bolbitis rhizophylla* (Kaulf.) Hennipman (*fide* Hennipman 1977).

Polybotrya serrulata Fée, Mém. Fam. Foug. (Hist. Acrost.) 76, pl. 39, fig. ii. 1845. = *Bolbitis rhizophylla* (Kaulf.) Hennipman (*fide* Hennipman 1977).

Polybotrya sinensis (Baker) C. Chr., Index Fil. 57. 1913. =*Bolbitis sinensis* (Baker) Iwatsuki (*fide* Hennipman 1977).

Polybotrya sorbifolia (L.) Keyserling, Pol. Cyath. Herb. Bung. 32. 1873. *nomen illegit.* =*Lomariopsis sorbifolia* (L.) Fée (*fide* Proctor 1977).

Polybotrya stenosemioides (Baker) Copel., Polypod. Philipp. 40. 1905. =*Heterogonium stenosemioides* (Baker) C. Chr. (*fide* Holttum 1975).

Polybotrya subquinquefida (Fée) Mettenius, Fil. Lechler. 2:12. 1859. =?*Leptochilus latifolium* (Meyen) C. Chr. (*fide* Christensen 1905).

Polybotrya taccaefolia (J. Smith) Mettenius, Fil. Lechler. 2:12. 1859. =*Leptochilus latifolius* (Meyen) C. Chr. (*fide* Christensen 1905).

Polybotrya tenuifolia (Desv.) Kuhn, Fil. Afr. 52. 1868. =*Stenochlaena tenuifolia* (Desv.) Moore (*fide* Christensen 1905).

Polybotrya teysmanniana (Baker) Posthumus, Rec. Trav. Bot. Neerl. 33:872. 1930. = *Stenosemia teysmanniana* (Baker) Diels (*fide* Christensen 1905).

Polybotrya trilobata (J. Smith) Mettenius, Fil. Lips. 24. 1856. =*Leptochilus latifolius* (Meyen) C. Chr. (*fide* Christensen 1905).

Polybotrya tripartita (Hooker & Grev.) J. Smith, Jour. Bot. 4:150. 1841. =*Peltapteris tripartita* (Hooker & Grev.) Morton (*fide* Morton 1955).

Polybotrya vivipara Hooker, Exotic Flora, 2: pl. 107. 1825. =*Bolbitis appendiculata* (Willd.) Iwatsuki subsp. *vivipara* (Hooker) Hennipman (*fide* Hennipman 1977).

Polybotrya wilkesiana Brackenridge, U.S. Expl. Exped. 16:80, tab. 10. 1854. =*Teratophyllum wilkesianaum* (Brackenridge) Holttum (*fide* Holttum 1978).

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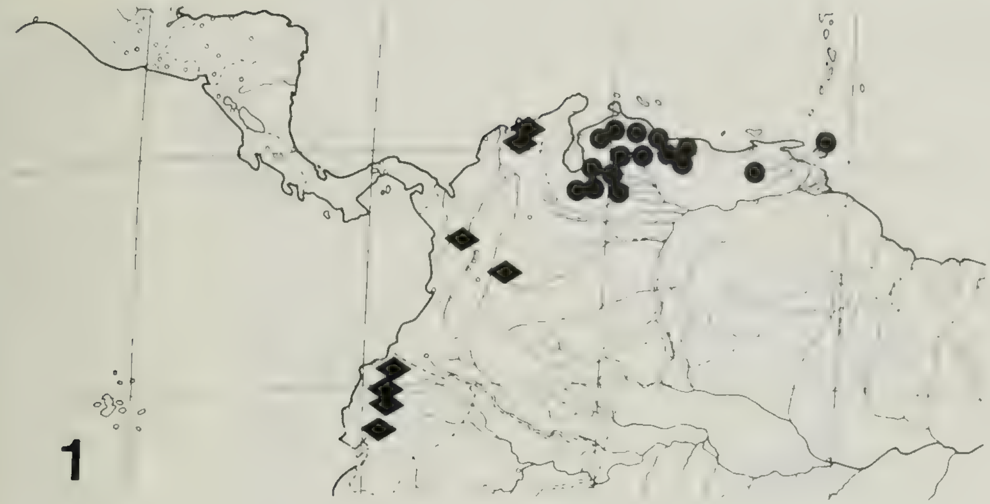
Taxa and Distribution of Polybotrya

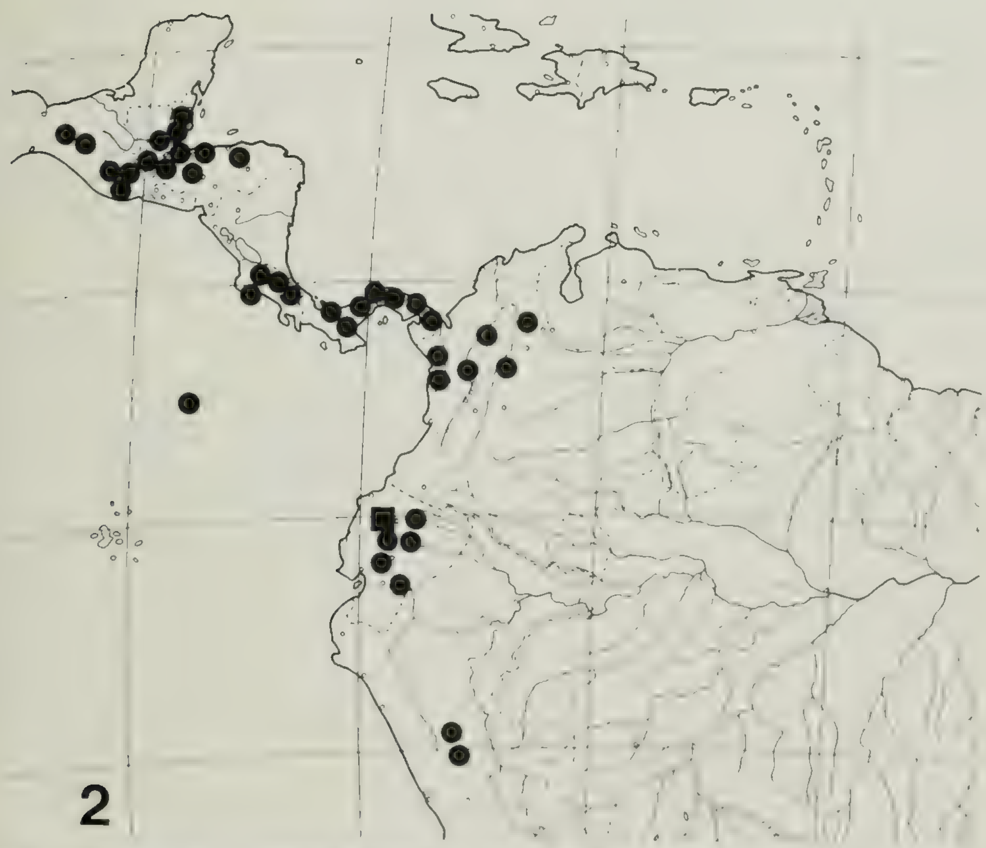
Numbers correspond to the species numbers assigned in the taxonomic treatment.

1. *Polybotrya serratifolia* (Fée) Klotzsch: Trinidad, Venezuela.
2. *Polybotrya polybotryoides* (Baker) Christ: Mexico, Belize, Guatemala, Honduras, Costa Rica, Panama, Colombia, Ecuador, Peru.
3. *Polybotrya suberecta* (Baker) C. Chr.: Colombia, Ecuador, Peru.
4. *Polybotrya andina* C. Chr.: Ecuador.
5. *Polybotrya sorbifolia* Kuhn: Costa Rica, Venezuela, Colombia, Brazil.
6. *Polybotrya fractiserialis* (Baker) J. Smith: French Guiana, Surinam, Guyana, Ecuador, Peru, Bolivia.
7. *Polybotrya crassirhizoma* Lellinger: Colombia, Ecuador, Peru, Bolivia, Brazil.
8. *Polybotrya espiritosantensis* Brade: Brazil.
9. *Polybotrya caudata* Kunze: Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Trinidad, French Guiana, Surinam, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil.
10. *Polybotrya goyazensis* Brade: Brazil, Paraguay.
11. *Polybotrya pubens* Martius: Colombia, Ecuador, Peru, Bolivia, Brazil.
12. *Polybotrya glandulosa* Kuhn: Venezuela, Peru, Brazil.
13. *Polybotrya lechleriana* Mettenius: Guyana, Colombia, Ecuador, Peru, Bolivia.
14. *Polybotrya attenuata* Moran: Colombia.
15. *Polybotrya stolzei* Moran: Colombia.
16. *Polybotrya alfredii* Brade: Nicaragua, Costa Rica, Panama, Ecuador, Peru, Bolivia.
17. *Polybotrya botryoides* (Baker) C. Chr.: Colombia.
18. *Polybotrya lourteigiana* Lellinger: Colombia.
19. *Polybotrya pittieri* Lellinger: Colombia.
20. *Polybotrya cylindrica* Kaulfuss: Brazil.
21. *Polybotrya hickeyi* Moran: Colombia, Bolivia.
22. *Polybotrya puberulenta* Moran: Ecuador, Bolivia.
23. *Polybotrya alata* Moran: Panama.
24. *Polybotrya aequatoriana* Moran: Ecuador, Bolivia.
25. *Polybotrya appressa* Moran: Ecuador.
26. *Polybotrya altescandens* C. Chr.: Colombia, Ecuador, Peru.
27. *Polybotrya gomezii* Moran: Costa Rica.
28. *Polybotrya osmundacea* Willd.: Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Cuba, Jamaica, Haiti, Grenada, Trinidad, French Guiana, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil.
29. *Polybotrya cyathifolia* Fée: Guadeloupe, Martinique.
30. *Polybotrya latisquamosa* Moran: Colombia.
31. *Polybotrya sessilisora* Moran: Colombia, Brazil.
32. *Polybotrya canaliculata* Klotzsch: Venezuela.
33. *Polybotrya semipinnata* Fée: Brazil.
34. *Polybotrya speciosa* Schott: Brazil.
35. *Polybotrya pilosa* Brade: Brazil.

Distribution Maps

The small open dots on the twenty-one distribution maps that follow indicate towns. Other symbols are explained in the legends.





MAP 1. Distribution of *Polybotrya suberecta* (Baker) C. Chr. (diamond) and *P. serratifolia* (Fée) Klotzsch (circle). MAP 2. Distribution of *Polybotrya polybotryoides* (Baker) Christ (circle) and *P. andina* C. Chr. (square).

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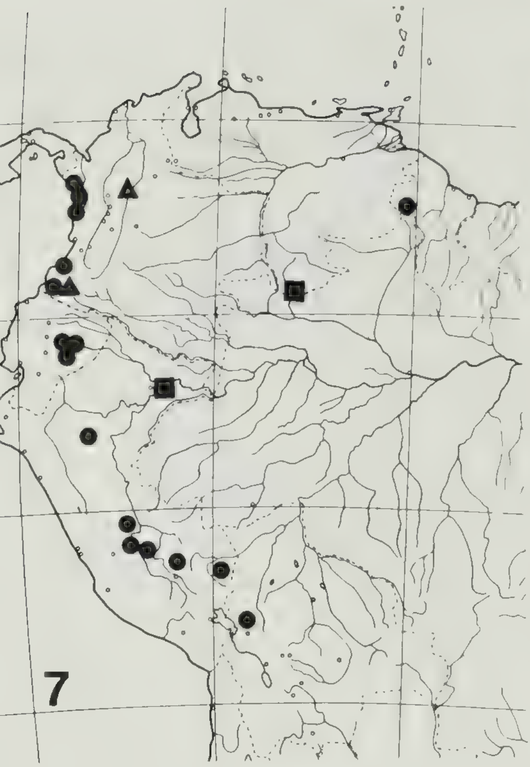
MAP 3. Distribution of *Polybotrya sorbifolia* Kuhn (diamond) and *P. fractiserialis* (Baker) J. Smith (circle). MAP 4. Distribution of *Polybotrya crassirhizoma* Lellinger.

MAP 5. Distribution of *Polybotrya caudata* Kunze. MAP 6. Distribution of *Polybotrya pubens* Martius (circle) and *P. goyazensis* Brade (diamond).



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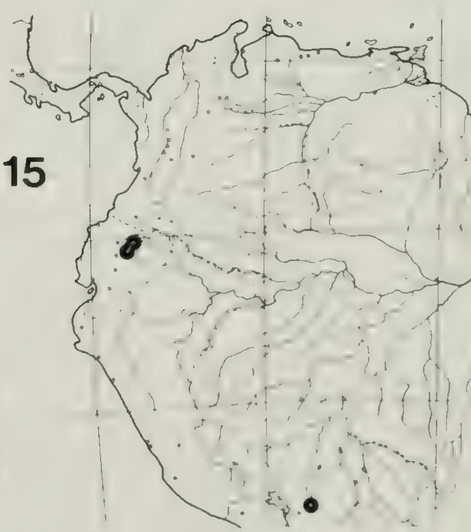
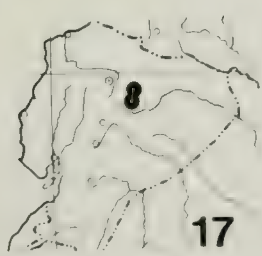
MAP 7. Distribution of *Polybotrya lechleriana* Mettenius (circle), *P. attenuata* Moran (triangle), and *P. glandulosa* Kuhn (square). MAP 8. Distribution of *Polybotrya alfredii* Brade (circle) and *P. botryoides* (Baker) C. Chr. (triangle). MAP 9. Distribution of *Polybotrya stolzei* Moran. MAP 10. Distribution of *Polybotrya lourteigiana* Lellinger. MAP 11. Distribution of *Polybotrya pittieri* Lellinger.





MAP 12. Distribution of *Polybotrya altescandens* C. Chr. MAP 13. Distribution of *Polybotrya hickeyi* Moran (circle) and *P. puberulenta* Moran (triangle). MAP 14. Distribution of *Polybotrya gomezii* Moran (circle) and *P. alata* Moran (triangle). MAP 15. Distribution of *Polybotrya aequatoriana* Moran. MAP 16. Distribution of *Polybotrya cylindrica* Kaulfuss. MAP 17. Distribution of *Polybotrya appressa* Moran.

MAP 18. Distribution of *Polybotrya osmundacea* Willd. (circle) and *P. semipinnata* Fée (triangle).
MAP 19. Distribution of *P. latisquamosa* Moran (solid square), *P. canaliculata* Klotzsch (triangle), and *P. cyathifolia* Fée (open square).

MAP 20. Distribution of *Polybotrya sessilisora* Moran (circle) and *P. pilosa* Brade (triangle).
MAP 21. Distribution of *Polybotrya speciosa* Schott (circle) and *P. espiritosantensis* Brade (triangle).

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Numbers in parentheses refer to the species numbers assigned in the taxonomic treatment.

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Almut G. Jones

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Aster and *Brachyactis* in Illinois

Almut G. Jones

Introduction

The need for a comprehensive study and taxonomic revision of asters in Illinois becomes apparent when one looks at the varied treatments of this genus in the principal floristic literature of the state (G.N. Jones 1945, 1950, 1963; Jones and Fuller 1955; Mohlenbrock 1975, 1986; Mohlenbrock and Ladd 1978). Three factors contribute to the differences found in these works: the number of taxa recorded for Illinois, nomenclatural considerations such as those dictated by the principle of priority, and differences in taxonomic concepts and interpretations.

In the first edition of *Flora of Illinois* (G.N. Jones 1945), 33 species are treated under *Aster*, not counting hybrids. Three additional species appear in the third edition (G.N. Jones 1963): *A. chasei* G.N. Jones in Jones & Fuller, a species newly described from Illinois; *A. tataricus* L.f., an occasionally escaped cultivated species; and *A. parviceps* (Burgess in Britton & Brown) Mack. & Bush, probably inadvertently omitted from the first two editions but included in Jones and Fuller (1955). In the most recent *Guide to the Vascular Flora of Illinois*, Mohlenbrock (1986) treats 35 species. A notable change involves the transfer of *A. ptarmicoides* (Nees) Torrey & Gray to *Solidago*. In this revision, I recognize 31 species of *Aster* in the state of Illinois.

My research has concentrated on New World and some Old World species of *Aster* (*sensu lato*) for over 15 years (A.G. Jones 1974, 1977, 1978a, b, c, 1980a, b, 1982, 1983, 1984, 1987; Jones and Hiepko 1981; Jones and Young 1983; Jones and Lowry 1986; and others), and much additional information has been introduced in this current study. My taxonomic concepts are summarized in the conspectus of classification of Illinois *Aster* species (p. 144).

A recent example of a name change necessitated by application of the principle of priority is that of *Aster azureus* Lindley in Hooker. The name is placed in synonymy under *A. oolentangiensis* Riddell (A.G. Jones 1983). Publication of the latter name preceded that of the former by only seven months. Other examples of name changes are *A. junciformis* Rydb. to *A. borealis* (Torrey & Gray) Prov., and *A. pantotrichus* S.F. Blake to *A. ontarionis* Wieg. (Shinners 1949).

Most differences among various accounts are attributable to disagreements about taxonomic concepts and interpretations. Changes may be the result of the union of two or more species under one [e.g., *Aster simplex* Willd. = *A. lanceolatus* Willd. (Semple 1979; Semple and Chmielewski 1987)], or they may involve elevation to the rank of species of taxa formerly considered at an inferior rank [e.g., *A. ericoides* L. (var.) *parviceps* Burgess in Britton & Brown = *A. parviceps*]. Sometimes names have been misapplied [e.g., *A. ericoides* for *A. pilosus* Willd. (cf. Blake 1930)], and occasionally a species is transferred to another genus [e.g., *A. ptarmicoides* to *Solidago* (Boivin 1972) and *A. brachyactis* S.F. Blake to *Brachyactis* (A.G. Jones 1984)].

The transfer of *Aster ptarmicoides* to *Solidago* is now generally accepted. Characters of habit, phyllaries, and achenes link this species [called Stiff

Aster by Swink (1974)] to the *Oligoneuron* group of *Solidago*. The genetic alliance is further supported by the fact that hybridization between *A. ptarmicoides* and species of the above group is not uncommon. One such hybrid has been reported from Cook County (Higley and Raddin 1891; Pepoon 1927; Jones and Fuller 1955; Swink 1974): *S.* × *lutescens* (Lindley in DC.) Boivin. It was first described as a species: *Diplopappus lutescens* Lindley in DC. [synonyms: *A. lutescens* (Lindley in DC.) Torrey & Gray; *A. ptarmicoides* var. *lutescens* (Lindley in DC.) A. Gray], and *S. riddellii* Frank is probably the other parent species involved in the hybrid.

Following my survey of the tribe Astereae (A.G. Jones 1984, 1985), I proposed returning *Brachyactis* Ledeb. to its originally published status as a separate genus. I have, however, included the single Illinois species *Brachyactis ciliata* (Ledeb.) Ledeb. in this study because it is considered a member of *Aster* in nearly all floristic literature to the present and because recent students of the taxon disagree with my viewpoint (Houle and Brouillet 1985).

Other recent treatments of *Aster* that espouse generic concepts different from mine have been published by Semple and Brouillet (1980a, b) and Reveal and Keener (1981). These treatments, however, which propose segregation from *Aster* of species of *A.* subg. *Virgulus* (Raf.) A.G. Jones ($x = 5$ chromosomes), have not been widely adopted. Evidence of hybridization between species of that assemblage and members of *A.* subg. *Symphyotrichum* (Nees) A.G. Jones ($x = 8$ chromosomes) supports a more conservative generic concept (A.G. Jones 1982; Jones and Young 1983; Allen 1985).

The following chapters are organized in the format used in most floristic manuals. The generic description of *Aster* (*sensu stricto*) is followed by a conspectus of classification of the Illinois species and by an indented key that includes both *Aster* and *Brachyactis*. Next, the species descriptions are given in alphabetic order by scientific name, the last being that of *Brachyactis ciliata*.

Within each entry, vernacular names used in literature dealing with the Illinois flora are listed after the scientific name. A new vernacular name is proposed (with some reluctance) in this work for *Aster fragilis* Willd.: **Brittle Aster**, a translation of the very appropriate specific epithet.

As much as possible, a uniform format is maintained in the descriptions. The diagnosis is followed by a listing of the mitotic ($2n$) chromosome number(s) and by those synonyms of the specific name that are cited for Illinois in other floristic works, including the bibliographic references.

A separate paragraph deals with phenology, ecology, and general geographic distribution. Standard two-letter postal abbreviations are used for names of the states and of the Canadian provinces, for example, AB (Alberta), NF (Newfoundland), PE (Prince Edward Island), PQ (Quebec), and YT (Yukon Territory).

Dot maps show the distribution of native Illinois species at the county level (county names are identified on the preceding map). These maps were based entirely on specimens I have examined, annotated, and recorded, and I may well have missed some counties for which valid records have been published. Previously published maps and lists, however, may include occasional recordings based on misidentifications. In addition to my own collections, I have examined more than 10,000 herbarium specimens for this study, including all material on deposit in the principal Illinois herbaria: DEK, EIU, F, ILL, ILLS, ISM, KNOX, MOR, MWI, and SIU. Abbreviations correspond to those in *Index Herbariorum* (Holmgren et al. 1981). GH, MIN, MO, NY, PH, US, and WIS are among the larger herbaria outside the state that yielded distribution data for the asters of Illinois. Some personal collections were borrowed from P. Shildneck and J. Schwegman.

Varieties are treated following the description of the respective species, either

in a short diagnostic statement or, in cases where a clear distinction by a combination of characteristics is possible, in the form of a key. Varietal synonymies are listed only to the extent that they have been cited for or described from Illinois. One reason for the inconsistency in the handling of varieties is that keys are not very meaningful or practical when a high degree of intergradation or overlap in characteristics exists. Moreover, I am convinced that some commonly recognized varieties have acquired their distinctive characteristics via gene flow from other species.

Hybrids are mentioned at the end of each entry, and some herbarium collections are listed as examples. Although only a few of the putative hybrids observed in the wild have been experimentally reproduced, the fact that closely related *Aster* species have a high degree of genetic homology and do occasionally hybridize is now generally accepted (Wiegand 1928, 1932; Cronquist 1947; Semple and Brammall 1982; and others). The classic example of an experimentally confirmed hybrid that may survive for several seasons is *A.* × *amethystinus* Nutt., pro sp. = *A. ericoides* × *A. novae-angliae* L. (Wetmore and Delisle 1939; A.G. Jones 1978c). At least some viable achenes are commonly produced, and backcrosses to plants of the parent species have been successful. Because of the relatively frequent occurrence of this hybrid, I have included it in the key and given a comparative description after that of one of its parent species (*A. novae-angliae*). Herbarium specimens of putative hybrid individuals, however, are not entirely uniform, and some are undoubtedly backcrosses to one or the other parent. Intergradation between two species is more evident in some cases than in others, and the key to the species generally does not work well for hybrids or for individuals that exhibit a high degree of introgression from other species.

Aside from the hybrid *Aster* × *amethystinus*, I have included in the key and discussed under their closest relatives two adventive species that may or may not be established in Illinois: *A. falcatus* Lindley in Hooker (under *A. ericoides*) and *A. ciliolatus* Lindley in Hooker (under *A. cordifolius* L.). I have also included the exotic species *A. tataricus* because it is treated in current manuals dealing with the flora of Illinois (Gleason 1952; Gleason and Cronquist 1963; G.N. Jones 1963; Mohlenbrock 1975, 1986).

Three species of *Aster* are included in the list of threatened species of Illinois issued by the Department of Conservation on March 14, 1989: *A. furcatus* Burgess in Britton & Brown, *A. schreberi* Nees, and *A. undulatus* L. In my opinion, *A. parviceps* should be considered for inclusion in the list. The latter species and *A. furcatus* are true midwestern endemics, and they may be threatened because the plants grow in vulnerable habitats. Although the number of locality records is considerable and some populations are extensive, these two species are probably not as common today as they used to be. I have been unsuccessful in my search in many places where they had been previously collected. The other two asters currently listed as threatened may be rare in Illinois, but they are very common in some other areas. Illinois populations represent the western limit of range for these species. *Aster schreberi* presents a special situation because Illinois and Wisconsin populations are disjunct from the nearest populations to the east and have been named and described as *A. chasei* (Jones and Fuller 1955). So far I have been unable, however, to find biological evidence that would support taxonomic recognition of these disjuncts as distinct from typical *A. schreberi*, even at the varietal rank. Other species that approach their limit of range in Illinois and are much more common outside the state are *A. borealis*, *A. dumosus* L., *A. macrophyllus* L., and *A. prenanthoides* Muhl. ex Willd.

To help resolve some of the difficulties of species delimitation that have haunted earlier accounts of *Aster*, I have made my keys and descriptions more detailed than

those generally found in floristic works. Many structural features that provide significant taxonomic information are often given short treatment because they are seasonal (e.g., those of mature fruits) or are not always available in herbarium specimens (e.g., rhizomes and basal rosettes). Because I have grown plants of all the species described here and observed them through the seasonal cycle, I have been able to characterize all structural elements. In addition to providing more complete descriptions of the species, this treatment will allow, at least in some cases, the detection of hybrids and populations showing intergradation.

The taxonomic method is an ongoing endeavor, and revisions are needed as more and more is learned about the genetics and natural history of the taxa. No doubt, the definitive account of *Aster* in Illinois will continue to elude us.

Acknowledgments

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Generic Description of *Aster* L.

Starwort, Wild Aster, Michaelmas Daisy, Frost-flower.

Herbaceous or somewhat suffruticose perennials with caudiciform or short to long-creeping stoloniform rhizome systems but also including some taprooted annuals (all native Illinois asters are perennial). **Stems** erect or decumbent, terete in cross section, or slightly ridged at the upper nodes from decurrent leaf bases, single to few at any point of emergence or cespitose, variously branched, glabrous to densely pubescent, sometimes glandular. **Leaves** simple, alternate, usually polymorphic, those of the basal rosettes and the lower stem often petiolate, those of the middle or upper stem and of the branches (rameal leaves) commonly subsessile or sessile; blades variously shaped, glabrous to densely pubescent, sometimes glandular, the apex acute, acuminate, attenuate, or obtuse to rounded, the margins entire, crenate, or serrate, never lobed, the base cuneate to rounded or cordate, sometimes sheathing or auriculate-clasping. **Capitulescence** paniculiform, corymbiform, racemiform, or rarely spiciform. **Heads** on short to long peduncles (sometimes subsessile), often secund from leaf axils of the terminal branchlets. **Involucre** cylindric, turbinate (often an artifact in pressed and dried specimens), campanulate, or hemispheric, the bracts (phyllaries) in several series. **Phyllaries** imbricated and usually graduated, occasionally subequal in length or the outer ones longer than the inner, commonly with a well-delimited apical green areole and a scarious, often indurate or keeled basal portion, or sometimes with green bands extending along the midrib to the base; phyllaries of the outer series often largely herbaceous. **Receptacle** flat or slightly convex, alveolate with blunt or sharp (rarely bristle-tipped) teeth or merely pitted in older, fruiting heads. **Ray florets** several to many, rarely absent or vestigial, mostly in 1 but sometimes in 2 or more series, pistillate and fertile, the strap-shaped or oblong ligule portion of the corollas white, pink, lavender, purple, or blue, never yellow, the tube portion yellowish green when fresh. **Disk florets** few to many, perfect and fertile, the corollas regular, cylindric or funnelform, usually with well-delimited tube and limb portions, the limb 5-lobed, cream-colored or yellow, often appearing brighter yellow before anthesis because of the presence of yellow pollen, commonly aging to pink or purple after the pollen is shed, the tube usually slender, yellow or greenish. **Style branches** of the disk florets with attenuate, papillate, sterile appendages that are longer than the stigmatic lines. **Pappus** often simple, composed of a single series of relatively uniform, barbellate, capillary bristles, or if more complex, either with 2 series of capillary bristles more or less uniform in length but with those of the inner series clavellately expanded toward the apex, or with an additional (third) outer series of distinct, very short, attenuate bristles (a feature conventionally referred to as a "double pappus"). **Achenes** plump or somewhat compressed, 2–5 times longer than wide, gray or straw-colored to purple or brown, glabrous to variously pubescent, with a species-specific, definite number (3–10) of ribs, these sometimes obscure. **Basic chromosome numbers**: $x = 5$, 8, and 9.

Excluded are *Aster brachyactis* S.F. Blake [= *Brachyactis ciliata* (Ledeb.) Ledeb.] and *A. ptarmicoides* (Nees) Torrey & Gray [= *Solidago ptarmicoides* (Nees) Boivin].

Aster can be distinguished from closely related genera (tribe Astereae) only by a combination of characteristics: sterile appendages of the style branches attenuate, longer than the stigmatic lines; phyllaries in 3 or more usually graduated series; rays never yellow; principal pappus bristles more or less uniform in length, not or scarcely overtopping the disk corollas; achenes usually with a definite number of ribs, not densely striated; flowering period typically late summer and fall.

Approximately 200 species, worldwide, mostly in the northern hemisphere, with the center of distribution in temperate North America. Taxonomic boundaries well defined in most species but blurred in some, largely as a result of interspecific hybridization, which is sometimes compounded by polyploidy. Moreover, the species exhibit a high degree of phenotypic variability, and similar morphologies may have evolved from different biological origins. Because many questions regarding the taxonomy of *Aster* cannot be answered at this time, the species concepts adopted in this treatment are relatively conservative.

Conspectus of Classification of Illinois *Aster* Species

Aster L.
- subgenus *Aster*
  - section *Biotia* DC. ex Torrey & Gray
    - *A. furcatus* Burgess in Britton & Brown
    - *A. macrophyllus L.*
    - *A. schreberi* Nees
  - sect. *Macrocephali* (Kitamura) A.G. Jones
    - *A. tataricus* L.f.
- subg. *Doellingeria* (Nees) A. Gray
  - sect. *Triplopappus* (Torrey & Gray) A.G. Jones
    - *A. umbellatus* Miller
- subg. *Ianthe* (Torrey & Gray) A. Gray
  - *A. linariifolius* L.
- subg. *Symphyotrichum* (Nees) A.G. Jones
  - sect. *Concinni* (Nees) Torrey & Gray
    - *A. laevis* L.
    - *A. oolentangiensis* Riddell
  - sect. *Cordifolii* G. Don in Loud.
    - *A. anomalus* Engelm. in Torrey & Gray
    - *A. ciliolatus* Lindley in Hooker
    - *A. cordifolius* L.
    - *A. drummondii* Lindley in Hooker
    - *A. shortii* Lindley in Hooker
    - *A. undulatus* L.
    - *A. urophyllus* Lindley in DC.
  - sect. *Dumosi* Torrey & Gray
    - *A. dumosus* L.
    - *A. fragilis* Willd.
    - *A. lateriflorus* (L.) Britton
    - *A. ontarionis* Wieg.
  - sect. *Porteriani* (Rydb.) A.G. Jones
    - *A. parviceps* (Burgess in Britton & Brown) Mack. & Bush
    - *A. pilosus* Willd.
  - sect. *Salicifolii* Torrey & Gray
    - *A. borealis* (Torrey & Gray) Prov.
    - *A. lanceolatus* Willd.
    - *A. praealtus* Poir.
    - *A. prenanthoides* Muhl. ex Willd.
    - *A. puniceus* L.
  - sect. ***Turbinelli*** (Rydb.) A.G. Jones, stat. and comb. nov.*
    - *A. turbinellus* Lindley in Hooker
- subg. *Virgulus* (Raf.) A.G. Jones
  - sect. *Concolores* Torrey & Gray
    - *A. sericeus* Vent.
  - sect. *Ericoidei* (Nees) Torrey & Gray
    - *A. ericoides* L.
    - *A. falcatus* Lindley in Hooker
  - sect. *Oblongifolii* (Rydb.) A.G. Jones
    - *A. novae-angliae* L.
    - *A. oblongifolius* Nutt.
  - sect. *Patentes* Torrey & Gray
    - *A. patens* Aiton

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* Based on *Aster* (species group) *Turbinelli* Rydb., *Flora of the Prairies and Plains*, 803, 804. 1932. Syn.: *A.* sect. *Eucephalus* subsect. *Turbinelli* (Rydb.) A.G.Jones (1980a). Type species: *A. turbinellus* Lindley in Hooker.

Key to Species of *Aster* and *Brachyactis* in Illinois

1. Plants annual with a taproot; rays absent or vestigial; pappus conspicuous at anthesis, considerably overtopping the corollas .... *Brachyactis ciliata*
1. Plants perennial (Illinois species); rays typically conspicuous; pappus relatively inconspicuous at anthesis, not or barely overtopping the disk corollas [*Aster*].
    2. Basal and lower cauline leaves long-petiolate, the blades well delimited, with mostly cordate to truncate or sometimes rounded bases.
        3. Capitulescence corymbiform or cymiform; median phyllaries mostly obtuse to rounded at the apex; disk corollas with the apparent tubular portion distinctly longer than the flared or abruptly expanded portion of the limb (including the lobes); achenes fusiform, with 7–10 (rarely more) ribs.
            4. Plants conspicuously glandular in the capitulescence .... 13. *A. macrophyllus*
            4. Plants typically not glandular (occasionally with a few glands on the peduncles and phyllaries).
                5. Rosettes of basal leaves prominent, often numerous forming a dense ground cover; blades of basal and larger cauline leaves broadly ovate to cordate, glabrous or with sparse indument, the petioles mostly much longer than the blades .... 24. *A. schreberi*
                5. Rosettes of basal leaves not prominent, relatively few; blades of basal and larger cauline leaves oblong-ovate or lanceolate, harshly scabrous above and densely hirsute below, the petioles usually not longer than the blades .... 8. *A. furcatus*
        3. Capitulescence variously paniculiform; median phyllaries acute, acuminate, or attenuate, or if obtuse, the apex with a sharp point, never rounded; disk corollas with the tube portion shorter than the expanded limb portion; achens oblong-obovoid, with 4 or 5(6) ribs.
            6. Phyllaries with strongly squarrose or reflexed tips; heads relatively large with (22)25–35 (or more) rays, the involucre hemispherical .... 1. *A. anomalus*
            6. Phyllaries with appressed or only slightly spreading tips; heads relatively smaller with ca 10–25 rays, the involucre campanulate or cylindrical (or turbinate in pressed specimens).
                7. Upper stem densely hirtellous or puberulent, the indument uniformly distributed around the stem; principal leaves copiously pubescent on both surfaces (or the upper surface glabrous in *A. shortii*).
                    8. Cauline leaves sessile and clasping or with auriculate-clasping petioles .... 30. *A. undulatus*
                    8. Cauline leaves not clasping, the petioles slender or winged, often somewhat decurrent but never clasping.
                        9. Leaves of the midstem entire or subentire; rays mostly (12)15–25; heads 1.5–2.5 cm in diameter when the rays are fully extended or pressed .... 26. *A. shortii*
                        9. Leaves of the midstem sharply serrate or crenate-serrate; rays mostly (8)10–15; heads 1–1.5(1.8) cm in diameter when the rays are fully extended or pressed .... 4. *A. drummondii*
                7. Upper stem glabrous or puberulent to villous in thin decurrent lines; principal leaves glabrous or variously pubescent.
                    10. Phyllaries of the 2nd and 3rd series inward with usually broad, short, rhombic green areoles; leaves of the midstem entire or subentire.
                        11. Leaves of the midstem auriculate-clasping, glabrous, glaucous .... 9. *A. laevis*
                        11. Leaves of the midstem not clasping, scabrous above and hirsute below, not glaucous .... 17. *A. oolentangiensis*

10. Phyllaries of the 2nd and 3rd series inward with obovate or usually narrower, lance-rhombic or oblanceolate to linear green areoles; leaves of the midstem variously toothed (sometimes subentire in *A. urophyllus*).
    12. Rays typically white (occasionally faintly lavender); phyllaries with a long-attenuate apex, largely scarious, often only the midrib light green, or the green areoles linear-oblanceolate .... 31. *A. urophyllus*
    12. Rays typically purple or lavender; phyllaries with variously shaped apices, the green areoles well developed, obovate or lance-rhombic to oblanceolate.
        13. Heads 1–1.5 cm in diameter when the rays are fully extended or pressed; total number of florets 16–30 (Illinois plants); apex of the phyllaries acute or sometimes short-acuminate .... 3. *A. cordifolius*
        13. Heads 1.5–2.5 cm in diameter when the rays are fully extended or pressed; total number of florets 30–50; apex of the phyllaries attenuate or narrowly acuminate .... 3a. *A. ciliolatus*

2. Basal and lower cauline leaves sessile to subpetiolate or if apparently petiolate, the blades with a cuneate base or gradually narrowed, not well delimited from the petiolar portion.
    14. Pappus with an outer whorl of very short bristles in addition to 1 or 2 series of much longer (principal) capillary bristles; leaves more or less uniform in contour except for the lowermost, which are usually bracteiform; basal rosettes absent.
        15. Leaves rigid, 1-nerved, lacking secondary nerves, ca 1–3.5 cm long and 0.4 cm or less wide; stems mostly less than 60 cm tall .... 12. *A. linariifolius*
        15. Leaves flexible, with well-developed secondary nerves, ca 4–12 cm long and 1 cm or more wide; stems mostly more than 60 cm tall .... 29. *A. umbellatus*
    14. Pappus simple, the bristles typically in a single series and more or less uniform in length; leaves usually variable in contour but the lowermost not bracteiform; basal rosettes present at least during part of the growing season.
        16. Involucres and peduncles, often also the leaves and upper stems, glandular.
            17. Rays (40)50–100; outer and median phyllaries narrowly acuminate to long-attenuate, strongly squarrose; cauline leaves auriculate-clasping .... 14. *A. novae-angliae*
            17. Rays 12–35; outer and median phyllaries obtuse or acute to short-acuminate, appressed or squarrose; cauline leaves variously inserted.
                18. Cauline leaves auriculate-clasping; phyllaries strongly graduated, appressed or with slightly recurved tips .... 19. *A. patens*
                18. Cauline leaves not or only slightly clasping, rounded at the base, not auriculate; phyllaries only slightly or not at all graduated, strongly squarrose .... 15. *A. oblongifolius*
        16. Involucres, peduncles, leaves, and stems not glandular.
            19. Achenes with 7–10 ribs, purple or brown at maturity; phyllaries pubescent on the outer (abaxial) surface; stem pubescence uniformly distributed around the stem, never in lines.
                20. Leaves and phyllaries appressed silvery-silky on both surfaces; ovaries and achenes glabrous .... 25. *A. sericeus*
                20. Leaves and phyllaries strigillose, hirsute, or cinereous-puberulent; ovaries and achenes pubescent.
                    21. Principal leaves auriculate-clasping; capitulescence an open, divaricately branched panicle; heads mostly on long, stiff peduncles, not crowded and not secund; rays purple .... 19. *A. patens*
                    21. Principal leaves rounded at the base, only slightly or not at all clasping; capitulescence commonly a racemiform panicle; heads subsessile or on relatively short peduncles, often crowded and secund; rays white or lavender.
                        22. Rays lavender; involucre hemispherical; pappus tawny or rose-tinged .... 14a. *A.* × *amethystinus*

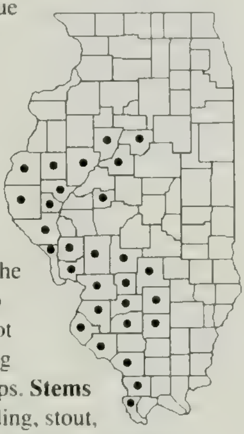
22. Rays typically white; involucre cylindrical to campanulate; pappus white or cream-colored.
    23. Heads commonly secund; involucres usually less than 4.5 mm high; rays 18 or fewer .... 6. *A. ericoides*
    23. Heads commonly not secund; involucres 5 mm high or more; rays 20 or more .... 6a. *A. falcatus* var. *commutatus*

19. Achenes with 3–5(6) ribs, variously colored; phyllaries mostly glabrous on the outer surface (rarely puberulent in a few species); stem pubescence variously distributed.
    24. Leaves clasping, often strongly auriculate.
        25. Leaves glaucous; stems glabrous or nearly so; phyllaries strongly graduated, firm, appressed when fresh, the apical green areole usually broad, rhombic, shorter than the scarious basal portion .... 9. *A. laevis*
        25. Leaves not glaucous; stems variously pubescent; phyllaries not at all or only weakly graduated, often flexible and leaflike, at least somewhat spreading or sometimes reflexed, the apical green areole longer than the scarious basal portion, or often the outer phyllaries largely herbaceous.
            26. Principal cauline leaves serrate to subentire, gradually tapered toward the base; stem variously hispidulous, as well as hirsute, either over the entire length and sometimes coarsely hispid toward the base, or often with only sparse hispidulous indument in the upper portion of the stem, the lower glabrous or nearly so (depending on the variety); phyllaries long-acuminate or attenuate .... 23. *A. puniceus*
            26. Principal cauline leaves sharply serrate, abruptly contracted below the middle into an entire-margined, sometimes apparently subpetiolar basal portion; stem hirsute or villous, not hispidulous; phyllaries acute or short-acuminate .... 22. *A. prenanthoides*
    24. Leaves not clasping.
        27. Involucre (7)8–12 mm high; phyllaries in 6–9 series, strongly graduated, blunt-tipped and rounded on the back, largely scarious, the green areoles small, oblong, in the apical 1/5–1/3 portion .... 28. *A. turbinellus*
        27. Involucre 3–8(10) mm high; phyllaries in 3–6 series, graduated to varying degrees, acute to attenuate or if obtuse, with a sharply pointed tip, not rounded on the back, the green areoles of various sizes and shapes.
            28. Basal leaves 3–4 times larger than the principal cauline leaves, the blades 10–30 cm long and 5–10 cm wide, gradually tapered into winged petioles 10–40 cm long; phyllaries with a broad green band along the midrib extending to the base .... 27. *A. tataricus*
            28. Basal leaves (often withered and deciduous at flowering time) mostly not larger than the principal cauline leaves, often much smaller; phyllaries usually with well-defined green areoles.
                29. Phyllaries and rameal leaves with a spinulose bristle at the apex; rhizome system caudiciform lacking stoloniform strands; new shoots initiated at the base of old stems or as root sprouts; achenes gray, the ribs obscure.
                    30. Disk florets 20 or more; involucre somewhat urceolate, (4)5–8 mm high .... 20. *A. pilosus*
                    30. Disk florets 6–12; involucre cylindric or turbinate, 3–4 mm high .... 18. *A. parviceps*
                29. Phyllaries and rameal leaves often with a sharp callus point at the apex but lacking a spinulose bristle; rhizome system creeping or if short-branched, the new shoots at least in part initiated at the ends of stoloniform rhizome strands; achenes variously colored at maturity, the ribs mostly prominent.
                    31. Reticulate tertiary venation usually conspicuous on the lower leaf surface, the veinlets often brownish, the enclosed green areolae isodiametric; rays purple or lavender .... 21. *A. praealtus*

31. Reticulate tertiary venation inconspicuous on the lower leaf surface, the veinlets rarely brownish, or the enclosed areolae oblong; rays variously colored.
    32. Ovaries and achenes glabrous, purple or brown at maturity, median phyllaries with mostly broad, short, rhombic (rarely lance-rhombic) green areoles; leaves scabrous above and hirsute below .... 17. *A. oolentangiensis*
    32. Ovaries and achenes strigillose or puberulent, variously colored at maturity; median phyllaries with linear, oblanceolate, or rhombic-obovate green areoles; leaves variously pubescent or glabrous.
        33. Lobes of the disk corollas longer than or as long as the fused portion of the limb (not including the corolla tube); lower leaf surface at least somewhat pubescent; achenes gray at maturity.
            34. Lower leaf surface uniformly short-pubescent; heads not secund; rhizomes distinctly long-creeping, stoloniform, the plants forming colonial stands, usually in moist ground .... 16. *A. ontarionis*
            34. Lower leaf surface villous to hirtellous along the midrib, otherwise usually glabrous; heads secund; rhizomes short, sometimes tangled but not long-creeping, the plants forming scattered individual clumps, mostly in upland situations .... 11. *A. lateriflorus*
        33. Lobes of the disk corollas shorter than the fused portion of the limb; lower leaf surface usually glabrous (rarely with a few trichomes along the midrib or slightly scabrous toward the margins); achenes variously colored.
            35. Flowering heads mostly 1.5–2.5 cm in diameter when the rays are fully extended or pressed.
                36. Larger cauline leaves 1–3.5 cm in width, no more than 12 times longer than wide, usually sharply serrate; capitulescence a diffusely branched or elongate panicle; achenes gray .... 10. *A. lanceolatus*
                36. Larger cauline leaves mostly less than 1 cm in width, 12–15 (or more) times longer than wide, shallowly and remotely serrate to subentire; capitulescence a more or less dichotomously branched round- or flat-topped panicle; achenes purple, or gray with purple streaks .... 2. *A. borealis*
            35. Flowering heads mostly 0.6–1.5 cm in diameter when the rays are fully extended or pressed.
                37. Median phyllaries (3rd or 4th series inward) ca twice as wide as those of the outer series, typically obtuse, the green areoles rhombic-obovate to broadly oblanceolate; rameal leaves relatively uniform in size; peduncles usually at least 1 cm long (often much longer) with many bracteiform leaves; subsessile heads relatively few .... 5. *A. dumosus*
                37. Median phyllaries slender, less than twice as wide as those of the outer series, acute or attenuate, the green areoles linear to narrowly oblanceolate; rameal leaves notably unequal in size; peduncles variable in length but the bracteiform leaves typically few; subsessile heads often numerous .... 7. *A. fragilis*

Description of *Aster* Species

1. *Aster anomalus* Engelm. in Torrey & Gray
Many-rayed Aster, Blue Aster

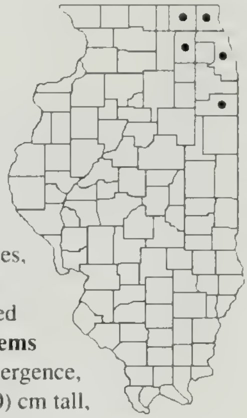


Herbaceous, with stout branched-caudiciform rhizomes that turn woody with age. **New shoots** arising at or near the base of old stems but also sometimes initiated as root sprouts, the plants forming scattered individual clumps. **Stems** 1–several, erect or ascending, stout, 50–120 cm tall, with ascending or spreading branches mostly from above the middle, uniformly hirtellous or hirsute. **Leaves** polymorphic, the basal and larger cauline ones petiolate, those higher up on the stem gradually reduced in size, changing from subpetiolate to sessile; first leaves of new shoots and of the vernal rosettes with oblong-ovate to lanceolate blades 1–4 cm long and 1–2 cm wide, usually purple at least on the lower surface, densely hirtellous, acute or often with obtuse to rounded tips, the margins few-toothed or subentire; principal cauline leaves with ovate to broadly lanceolate blades 4–9 cm long and (1.5)2.5–5 cm wide, with several pairs of usually arching and anastomosing secondary nerves, hirtellous or hirsute on both surfaces, the apex acute or acuminate with a short callus point, the margins mostly entire to subentire (rarely crenate-serrate), the base cordate, usually with broad sinuses (rarely truncate), the petioles (2)4–8 cm long, slender on the lower leaves, narrowly winged on those of the midstem, densely hirsute to pilose; upper leaves of the main stem lanceolate, entire; rameal leaves abruptly reduced, those of the peduncles bracteiform, 2–6 mm long, mucronulate, intergrading with the phyllaries. **Capitulescence** a usually ample diffuse panicle, the head-bearing branchlets sometimes racemiform. **Flowering heads** 2–3 cm in diameter when the rays are fully extended, on peduncles 0.3–5(10) cm long or rarely subsessile. **Involucre** hemispherical, 5–10 mm high, the phyllaries imbricated in 4–6(7) series. **Phyllaries** graduated, slender, linear-lanceolate, strongly reflexed or squarrose, grayish green, both surfaces typically hirtellous, the apex long-attenuate, often with purple tips and with a conspicuous bristly mucro, the margins scabrous; outer phyllaries 3–4 mm long, ca half as long as the inner, commonly herbaceous to near the base; median and inner phyllaries green in the apical $^1/_2$–$^2/_3$ portion, the basal portion scarious. **Receptacle** alveolate with sharp or bluntish teeth. **Ray florets** (22)25–35 (or more), the corollas 10–15(18) mm long, purple or blue (rarely white), glabrous. **Disk florets** 20–35 (or more), the corollas (4)4.5–5.5 mm long, glabrous or with a few trichomes, the limb only slightly expanded, cream-colored or light yellow turning purple after anthesis, the lobe/limb fraction 0.2–0.25, the tube shorter than the limb. **Pappus** simple, the bristles as long as the disk corollas or slightly shorter, tawny or rose-tinged, slender, attenuate. **Achenes** oblong-obovoid, somewhat compressed, 2.5–3.5(3.8) mm long and 0.8–1.2 mm across, deep purple, or brown with purple speckles, glabrous, with 5 or 6 often irregularly spaced straw-colored ribs. $2n = 16$; reported chromosome counts of $2n = 18$ are probably in error (A.G. Jones 1977, 1980b).

Late August–October. Sandy or loamy clay soils underlain by calcareous rocks or sandstone: rocky open woods, woody hilltops, and dry ridges. Occasional near and along major rivers in the western half of the state, north to Peoria and Woodford counties. The range for the species includes MO, AR, s.e. KS, and e. OK.

There is good evidence in Illinois of intergradation between this species and *Aster shortii* [e.g., *Winterringer 11997* (ISM) from Alexander Co., *Rexroat 8084* (ISM) from Menard Co., and *A.G. Jones 6817* (ILL) from Union Co.].

2. *Aster borealis* (Torrey & Gray) Prov.
Rush Aster



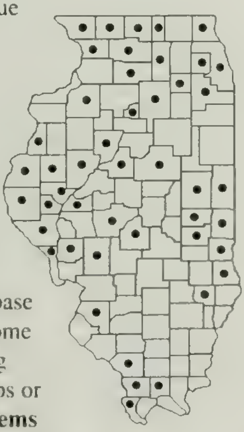
Herbaceous, with very slender, creeping, stoloniform rhizomes. **New shoots** mostly initiated from the rhizomes, the plants forming clonal stands usually interspersed with other vegetation. **Stems** 1–few at any point of emergence, slender, erect, 30–80(100) cm tall, often somewhat zigzag above, branched only in the capitulescence, sometimes red-tinged to slightly glaucous, nearly glabrous or sparsely puberulent in thin decurrent lines (rarely with uniformly distributed indument on the peduncles). **Leaves** polymorphic, the basal and lower cauline ones commonly withered and deciduous at flowering time; basal rosette leaves subpetiolate, the blades variously linear-oblanceolate to ovate or suborbiculate, 0.5–1.5 cm long and 2–6 mm wide, the secondary venation obscure, both surfaces glabrous or minutely puberulent toward the margins, the lower surface also usually purple-tinged, the apex obtuse or rounded, the margins shallowly crenate, abruptly narrowed to a slightly winged subpetiolar portion of variable length, the base dilated and sheathing; principal cauline leaves very slender, linear to linear-oblanceolate, (4)6–15 cm long and 2–6(8) mm wide, with usually only the midrib strongly expressed, glabrous or the upper surface minutely strigillose toward the margins and the lower with a few trichomes along the midrib, the apex attenuate and callus-pointed, the margins usually inrolled, entire or remotely and shallowly serrate, smooth or scabrous, the base sessile and somewhat decurrent; rameal leaves relatively few, ascending or spreading, firm or flexible, entire, similar to the cauline leaves in contour and vestiture, the base somewhat sheathing and decurrent; leaves of the peduncles flexible, not phyllarylike, linear-lanceolate, 4–12 mm long, often red-tinged, and with a slightly dilated or rounded base. **Capitulescence** an open, round- or flat-topped, more or less dichotomously branched, terminal panicle, rarely also with ascending lateral branches initiated in leaf axils of the midstem. **Flowering heads** (1.5)2–2.5 cm in diameter when the rays are fully extended, not crowded and not secund, typically on slender puberulent or glabrous peduncles 1–5 cm in length. **Involucre** broadly campanulate, (5.5)6–7 mm high, the phyllaries imbricated in 4–6 series. **Phyllaries** appressed when fresh or rarely the outermost slightly recurved, subequal or somewhat graduated; outer phyllaries oblong-lanceolate, 3–5 mm long, the innermost slender, linear, 5–6 mm long, the green areoles changing from slenderly oblanceolate to nearly linear, the surfaces glabrous or nearly so, the apex acute, callus-pointed in the outer phyllaries, often red-tipped in the median and inner ones, the margins irregularly ciliolate (rarely villous), or erose-hyaline and with a scarious or reddish rim in the median and inner phyllaries, the basal $^{1}/_{2}$–$^{2}/_{3}$ portion scarious. **Receptacle** shallowly alveolate with sharp teeth. **Ray florets** 20–30 (or more), the corollas 10–12 mm long, mostly white, sometimes pink or bluish, glabrous or with a few trichomes at the throat and on the tube. **Disk florets** 25–30 (or more), the corollas funnelform, 5–6 mm long, glabrous or nearly so, the limb abruptly expanded at the throat, cream-colored or pale yellow turning pink after anthesis, the lobe/limb fraction 0.2, the tube shorter than the limb. **Pappus** simple, the bristles approximately as long as the disk corolla, whitish, soft, slender, and attenuate. **Achenes** oblong or oblanceolate in contour or often somewhat falcate, plump or slightly compressed, (2.2)2.5–3 mm long, 4–5 times longer than wide, purple, or gray with purple streaks, thinly strigillose, with 4 or 5 straw-colored ribs. $2n$ = 16, 32 (mostly), 48. [*A. junceus* misapplied, not of Aiton—Brendel 1887; Pepoon 1927; Deam 1940. *A. junciformis* Rydb.—G.N. Jones 1945, 1950, 1963; Fernald 1950; Gleason 1952; Jones and Fuller 1955; Gleason and Cronquist 1963; Swink 1974; Mohlenbrock 1975; Swink and Wilhelm 1979.]

Late August–October. Wet ground: tamarack bogs, sedge meadows, grassy lakeshores, and calcareous fens. Occasional in the counties including and surrounding Chicago, now probably rare because of destruction of the habitat. The species range is still to be accurately mapped. I have been unable, for example, to locate the specimen cited for Winnebago County by Fell (1955: 144) under the name *Aster junciformis;* the descriptive statement suggests that the plant (found "in boggy places in Coon

Creek bottom") may belong here. According to the floristic literature, the species has been recorded from Anticosti Island, NB, and PQ, westward through ON, MB, SK, s. NT, and s. YT to BC and s. AK, southward to areas surrounding the Great Lakes in NY, PA, OH, and IN, and also including stations in n. IA, ND, SD, n. NE (?), and MT. Excluded are some areas listed in the literature for which the recorded specimens, in my judgment, belong in other species.

The plants may be confused with those of some other species, e.g., *Aster dumosus* var. *strictior* Torrey & Gray, but the latter taxon is distinct by having smaller heads and a strict, thyrsiform capitulescence. The characteristics of *A. borealis* suggest a close relationship in the eastern half of the continent to *A. lanceolatus* and *A. longifolius* Lam., and in the western half to *A. eatonii* (A. Gray) Howell and *A. occidentalis* (Nutt.) Torrey & Gray. Of these four species only *A. lanceolatus* is an element of the Illinois flora, and good evidence exists of intergradation between that species and *A. borealis* [e.g., *Benke 5278* (F) from McHenry Co.].

3. *Aster cordifolius* L.
Heart-leaved Aster, Blue Wood Aster



Herbaceous, with a branched-caudiciform or creeping horizontal rhizome system (depending on the variety). **New shoots** originating at the base of old stems or from rhizome strands, the plants forming scattered individual clumps or small colonial patches. **Stems** 1–several, erect, (40)60–120 cm tall, often reddish or maroon-colored, commonly somewhat zigzag above, with ascending or divaricate branches from above the middle, typically puberulent in decurrent lines from the upper nodes, in the leaf axils, and on the peduncles, glabrous in the lower stem portion (sometimes entirely glabrous). **Leaves** polymorphic, the basal and principal cauline ones petiolate, those higher up on the stem gradually reduced in size, changing to subsessile or sessile in the branches; leaves of new shoots and of the vernal rosettes with ovate-cordate to suborbiculate blades 1–8 cm (or more) long and 1–3 cm (or more) wide, similar to the cauline leaves in venation and vestiture, purplish below at least during the cool season, the apex acuminate or acute (sometimes obtuse or rounded), the margins coarsely and often irregularly crenate-serrate, the base cordate (rarely rounded), the petioles 1–3 times as long as the blades, ciliate, slender or often winged, dilated toward the sheathing base; blades of principal cauline leaves ovate in contour, 4–10(13) cm long and 2–4(6) cm wide, with several pairs of arching and anastomosing secondary nerves, and a weakly expressed reticulum of tertiary veins with irregular areolae, the upper surface sparsely scabrous or glabrous, the lower thinly villous or hirtellous along the major nerves (rarely over the entire surface) or nearly glabrous, the apex acuminate and callus-pointed, the margins sharply serrate with acuminate callus-pointed teeth, the base deeply cordate or truncate to rounded, the petioles progressively shorter and more broadly winged upward on the stem; rameal leaves subsessile to sessile, ovate-lanceolate, nearly glabrous or minutely puberulent above, acuminate and callus-pointed, the margins entire or commonly somewhat toothed and ciliolate; leaves of the peduncles densely spaced, 1.5–3 mm long, the lower ones flexible, the upper bracteiform and intergrading with the phyllaries. **Capitulescence** a leafy, divaricately much-branched, usually round-topped panicle in the upper $\frac{1}{4}$–$\frac{1}{2}$ portion of the stem, the head-bearing branchlets rarely racemiform. **Flowering heads** 1–1.5 cm in diameter when the rays are fully extended, often crowded, usually not secund, on densely bracteate peduncles 0.3–2 cm long. **Involucre** narrowly campanulate (sometimes turbinate when pressed and dried), 3.5–5(6) mm high, the phyllaries imbricated in (3)4 or 5 series. **Phyllaries** strongly graduated, the outer ones lanceolate, (1)1.5–2 mm long, the inner slender, linear-oblanceolate, 3.5–4.5(5) mm long, appressed when fresh, glabrous, the green areoles rhombic to obovate and well delimited in the apical $\frac{1}{4}$–$\frac{1}{2}$ portion, commonly red-tipped, the apex typically acute or obtuse (rarely acuminate) in the outer and median, acuminate to short-attenuate in the inner phyllaries, the

margins erose-hyaline, irregularly ciliolate or thinly villous toward the apex, the basal portion scarious, often somewhat rounded on the back and indurate. **Receptacle** alveolate with sharp teeth. **Ray florets** (8)10–15, the corollas 7–10 mm long, typically purple (rarely pink), glabrous or nearly so. **Disk florets** (8)10–12, the corollas 4–4.5(5) mm long, funnelform, glabrous or with a few trichomes at the throat, the limb abruptly dilated, cream-colored or light yellow turning purple after anthesis, the lobe/limb fraction 0.2–0.25, the tube slightly shorter than the limb. **Pappus** simple, the bristles as long as or slightly shorter than the disk corolla, whitish or faintly rose-tinged, soft, slender, and attenuate. **Achenes** oblong-obovoid or often slightly falcate, somewhat compressed, 2–2.5 mm long and 0.6–0.8 mm across, dull purple or light brown, glabrous, with 4 or 5 ribs. $2n = 16, 32$ (often with 1 or 2 B-chromosomes); reported chromosome counts of $2n = 36$ are probably in error (A.G. Jones 1977). Including *A. sagittifolius* Wedem. ex Willd. (*sensu stricto*—A.G. Jones 1980b, 1987; Jones and Hiepko 1981).

September–October. Loamy or rocky soils in mesic, mostly wooded habitats: open-wooded slopes and bluffs, woodland edges, also in somewhat disturbed ground at road cuts and along ditches. Occasional throughout the state but more common in the northern part. The range of this variable species extends from PE, PQ, NB, NS, and ME south to GA and AL, westward to MN, IA, e. NE, MO, and AR.

Two varieties can be distinguished in Illinois, typical var. *cordifolius* and *Aster cordifolius* var. *sagittifolius* (Wedem. ex Willd.) A.G. Jones [*A. sagittifolius* of authors only in part (see also *A. drummondii* and *A. urophyllus*); *A. cordifolius* subsp. *sagittifolius* (Wedem. ex Willd.) A.G. Jones (1980b)]:

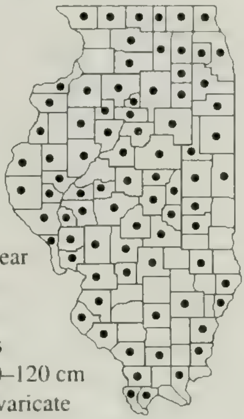
1. Rhizomes notably creeping, with slender stoloniform strands, the plants colonial; leaves of the midstem with slender or narrowly winged petioles, the blades with a deeply cordate base .... var. *cordifolius*
1. Rhizomes short, branched-caudiciform, the plants forming scattered individual clumps; leaves of the midstem with broadly winged petioles, the blades with a truncate or shallowly cordate base ....var. *sagittifolius*

Plants of var. *sagittifolius* exhibit traits that may have been acquired via gene flow from other species, such as *Aster ciliolatus* and *A. drummondii*. If underground parts are missing, specimens of this taxon can be distinguished only with difficulty from those of typical var. *cordifolius*. There is evidence of intergradation between *A. cordifolius* and *A. drummondii* [e.g., *Henry 2941, 2943* (MWI) from Adams Co. and *Chase 14906* (ILL) from Peoria Co.], *A. laevis* [e.g., *Chase 3728* (ILL) from Tazewell Co.], and *A. urophyllus* [e.g., *Evers 58628* (ILLS) from La Salle Co. and *Fuller & Fisher 353, 370* (ISM) from Union Co.].

3a. *Aster ciliolatus* Lindley in Hooker
Lindley's Aster

I have included this species in the key on the strength of three herbarium specimens collected in Cook County and located at F [*R. Bebb 1570*, Beverly Hills; *F. Gates 43*, Glencoe; *Raddin s.n.*, n. Evanston]. The plants more or less exhibit the traits attributed to *Aster ciliolatus*: stems glabrous or nearly so; principal leaves glabrous or sparsely ciliate below along the major nerves; peduncles with no or few bracteiform rameal leaves; heads relatively large, the involucres 6–7 mm high; phyllaries lanceolate, long-attenuate, with lance-rhombic green areoles and indurate, scarious or somewhat discolored bases. In fact, the Gates collection was annotated by Sherff as *A. lindleyanus* Torrey & Gray, a synonym of *A. ciliolatus*. Field study is needed to ascertain whether this transcontinental boreal species is really an established element of the Illinois flora. The plants may be waifs, or they may be part of a hybrid swarm involving *A. cordifolius* and *A. ciliolatus* (or some other species, e.g., *A. laevis*).

4. ***Aster drummondii*** Lindley in Hooker
Drummond's Aster

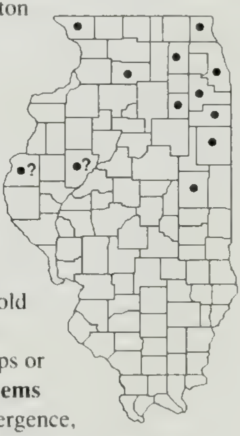


Herbaceous, with stout branched-caudiciform rhizomes that often turn woody with age. **New shoots** originating at or near the base of old stems, the plants forming scattered individual clumps. **Stems** 1–several, erect, stout, 60–120 cm tall, with ascending or divaricate branches mostly from above the middle, uniformly soft-hirtellous in the branches, coarsely hirsute on the main stem, the indument often in lines, sometimes glabrescent in the lower portion. **Leaves** polymorphic, the basal and lower cauline ones petiolate, those higher up on the stem gradually or abruptly reduced in size; leaves of new shoots and vernal rosettes with ovate-oblong to suborbiculate blades 1–6(10) cm long and 1–3(5) cm wide, purplish below at least during the cool season, copiously soft-pubescent on both surfaces, the apex acute, obtuse, or rounded, the margins crenate-serrate; principal cauline leaves with broadly ovate to ovate-lanceolate blades 6–12(15) cm long and 3–5(6) cm wide, with 5–12 pairs of arching and anastomosing secondary nerves, thinly soft-pubescent to scabrous or rarely glabrous above, copiously hirtellous to hirsute below, the apex acuminate to attenuate and usually callus-pointed, the margins crenate-serrate to sharply (sometimes doubly) serrate, the base cordate or truncate, sometimes oblique; petioles (2)4–8 cm long, usually conspicuously winged and with ciliate margins; upper leaves of the main stem lanceolate, subsessile; rameal leaves oblong-lanceolate, sessile, typically pubescent, callus-pointed, shallowly toothed to entire and ciliolate; leaves of the peduncles bracteiform, 2–5 mm long, intergrading with the phyllaries. **Capitulescence** a usually ample panicle, distinctly overtopping the leafy stem portion, the terminal branchlets often racemiform. **Flowering heads** 1–1.5(1.8) cm in diameter when the rays are fully extended, on densely bracteate peduncles 0.2–4 cm long, or sometimes subsessile and secund. **Involucre** campanulate (or turbinate when pressed and dried), (3.5)4–6 mm high, the phyllaries imbricated in (3)4 or 5 series. **Phyllaries** strongly graduated, the outer ones lanceolate or subulate, 1.5–2 mm long, the inner linear-lanceolate, ca three times as long as the outer, appressed or slightly spreading, typically glabrous but occasionally puberulent on the abaxial surface and thinly puberulent on the adaxial surface, the apical green areoles rhombic to oblong or oblanceolate, the apex acuminate or attenuate, often red-tipped, the margins irregularly ciliolate toward the apex, and with a scarious rim extending to the tapered portion of the tip, the basal $^{1}/_{4}$–$^{1}/_{2}$ portion scarious except for the often green midrib. **Receptacle** shallowly alveolate with sharp or blunt teeth. **Ray florets** (8)10–15 (or more), the corollas 7–12 mm long, purple or lavender (sometimes white), glabrous. **Disk florets** (10)13–15 (or more), the corollas 3.5–4.5(5) mm long, funnelform, glabrous, the limb abruptly dilated at the throat, cream-colored or light yellow turning deep purple after anthesis, the lobe/limb fraction 0.18–0.25, the tube slender, slightly shorter than the limb. **Pappus** simple, the bristles subequal, slightly shorter than the disk corolla, whitish or rose-tinged, soft, slender, and attenuate. **Achenes** oblong-obovoid, often slightly falcate, somewhat compressed, (1.5)2–3 mm long and 0.6–1 mm across, dull purple or brown, glabrous or often sparsely puberulent in the top portion, with 4 or 5 ribs. $2n = 16, 32$ (mostly); reported chromosome counts of $2n = 36$ are probably in error (A.G. Jones 1977). [*A. sagittifolius* Wedem. ex Willd. var. *drummondii* (Lindley in Hooker) Shinners—Fernald 1950; Kibbe 1952; Dobbs 1963; Swink 1974; Mohlenbrock 1975; Swink and Wilhelm 1979. *A. undulatus* misapplied, not of L.—Mead 1846; Higley and Raddin 1891; Pepoon 1927; Kibbe 1952; Dobbs 1963.]

August–October. Loamy or rocky soils in mesic, mostly wooded habitats: stream banks, open-wooded slopes, thickets and edges of swamps; also sometimes in disturbed ground along roads and ditches. Common throughout the state. The range of this variable species extends from s. MN east to c. OH, south to w. MS, n. LA, and e. TX, and west to IA, e. NE, e. KS, and e. OK.

Plants in Illinois belong mostly in typical var. *drummondii*, including *Aster drummondii* var. *rhodactis* Benke, described from Cook County [*Benke 4830* (F)] and characterized by rose-colored rays and "rufescent" leaves and stems. Individuals exhibiting phyllaries that are puberulent on the back may fall within the limits of *A. finkii* Rydb., a species (or more likely a hybrid) described from Iowa and recognized by Shinners (1941) as an endemic of the driftless area of s.w. WI. I have recorded collections of these plants from 16 counties throughout the state and did not detect geographic or ecological patterns or any consistent correlation of this trait with other characters. Occasional hybridization with and gene flow from *A. shortii* or *A. undulatus* (or both) may in part account for the occurrence of puberulent phyllaries in *A. drummondii*. I find it impossible, therefore, to give taxonomic recognition to this morphological variant. There is also strong evidence of intergradation between *A. drummondii* and *A. urophyllus* [e.g., *Evers 28089* from Jo Daviess Co., *28300* from Pope Co., *71937* from Adams Co., and *77383* from Lee Co. (all at ILLS)].

5. *Aster dumosus* L. var. ***strictior*** Torrey & Gray
Bushy Aster, Rice-button Aster



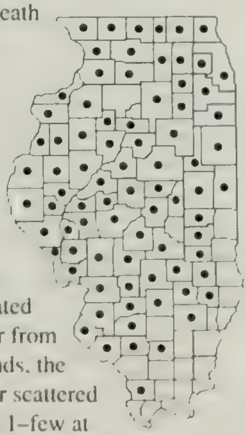
Herbaceous, with a creeping stoloniform rhizome system. **New shoots** mostly initiated from the rhizomes or sometimes at the base of old stems, the plants forming scattered individual clumps or small colonial patches. **Stems** 1–few at any point of emergence, slender, erect, 30–70(100) cm tall, terete, the branches commonly ascending (this variety), sometimes divaricate, slightly ridged from decurrent leaf bases, sparsely puberulent in lines or nearly glabrous, the indument more copious on the peduncles and sometimes uniformly distributed. **Leaves** somewhat polymorphic, the basal and larger ones mostly withered and deciduous at flowering time; basal rosette leaves spatulate, 1–5 cm long, glabrous or minutely scabrous above, usually purple-tinged below, crenate-serrate, abruptly narrowed to a coarsely ciliate subpetiolar portion, dilated and sheathing at the base; principal cauline leaves linear to linear-oblanceolate, 3–10 cm long and 2–3(5) mm wide, with (usually) only the midrib strongly expressed, scabrous or glabrescent above, glabrous below, the apex acute with a sharp callus point, the margins usually inrolled, scabrous, shallowly serrulate or rarely entire, the base sessile and often somewhat decurrent but not clasping; rameal leaves numerous, bracteiform, linear-oblong, rather uniform in size at each branch level and with relatively few clusters of smaller leaves in the axils, ascending or spreading, scabrous-margined, and callus-pointed, those of the peduncles densely spaced, 1–3 mm long, intergrading with the phyllaries. **Capitulescence** a narrow panicle with stiffly ascending racemiform branches above the middle, or sometimes more broadly and diffusely branched from the lower nodes. **Flowering heads** 0.8–1.5 cm in diameter when the rays are fully extended, typically on slender, puberulent or glabrous peduncles 1–5 cm (or more) in length (rarely subsessile). **Involucre** 3–5 mm high, narrowly campanulate (or turbinate when pressed and dried), the phyllaries imbricated in 4 or 5 series. **Phyllaries** strongly graduated, appressed or slightly spreading, glabrous on the abaxial surface but often with a few trichomes on the adaxial surface, the green areoles well delimited, rhombic-obovate to broadly oblanceolate, the apex obtuse or acute, the margins irregularly ciliolate, hyaline, and also with a scarious rim, the basal $^2/_3$ portion scarious except for the often slightly keeled green or brown midrib; outer phyllaries 1–1.5 mm long, oblong-lanceolate, those largest in surface area (3rd or 4th series inward) more than twice as long and ca twice as wide as the outer ones, linear or somewhat expanded toward the apex; innermost phyllaries very slender. **Receptacle** shallowly alveolate with sharp teeth. **Ray florets** 15–25 (or more), the corollas 4–6(8) mm long, typically pink or lavender (sometimes white), glabrous. **Disk florets** 15–20 (or more), the corollas narrowly funnelform, 3.5–4.5 mm long, glabrous, the limb cream-colored or light yellow turning pink after anthesis, the lobe/limb fraction 0.25–0.35, the tube shorter than the limb. **Pappus** simple, the bristles approximately as long as the disk corolla, whitish, soft, slender, and attenuate. **Achenes** oblong-obovoid, plump or slightly compressed, 1.5–2.5 mm long and 0.5–0.7 mm across, pink, or

straw-colored with pink streaks, strigillose and sometimes minutely puncticulate, with 3–5 prominent ribs, the sculpturing conspicuous even in immature ovaries. $2n = 16, 32$, sometimes with additional B-chromosomes.

Late August–October. Moist or wet ground: bogs and sandy or calcareous flats. Not common in Illinois; apparently concentrated in the northeastern part of the state, south to Champaign County and west to Lee County. Collections recorded from Hancock and Jo Daviess counties may belong in or near *Aster fragilis* rather than *A. dumosus*. Our records mark the northwestern limit for this extremely variable species, the range of which extends from ME to s. ON, MI, and s. WI, south to s. FL and LA, and southwest to MS, AR, the s.e. corner of OK, and e. TX.

Good evidence suggests intergradation between this taxon and the often sympatric populations of *Aster fragilis* [e.g., *A.G. Jones 3303* (ILL) from Iroquois Co.] and *A. lanceolatus* var. *interior* (Wieg.) Semple & Chmielewski [e.g., *A.G. Jones 3304* (ILL) from Iroquois Co. and *E.J. Hill 100, 1884* (ILL) from Cook Co.]. In fact, all characteristics that, according to Torrey and Gray (1841) and Wiegand (1928), distinguish *A. dumosus* var. *strictior* from typical var. *dumosus* may be traceable to similar characteristics in one or both of the above-mentioned taxa, e.g., the "strict" branching habit, the often racemiform and relatively short-peduncled exposition of heads, and the comparative paucity of indument. These species are closely related and share a basic chromosome number of $x = 8$.

6. *Aster ericoides* L.
White Prairie Aster, Heath Aster, Wreath Aster



Herbaceous, with a strongly creeping (Illinois plants) or short caudiciform rhizome system, depending on the variety. **New shoots** initiated at the base of old stems or from stoloniform rhizome strands, the plants forming colonies or scattered individual clumps. **Stems** 1–few at any point of emergence, erect, the branches ascending or often somewhat fastigiate and arching, 30–80(100) cm tall, uniformly and often harshly pubescent, the trichomes appressed-strigose, ascending, or spreading to reflexed hirsute (depending on the variety), the lower stem portion sometimes glabrescent. **Leaves** numerous, firm, sessile, entire, variously pubescent on both surfaces, often with clusters of smaller leaves at the nodes and in the axils of the larger ones, commonly all except the rameal leaves withered and deciduous at flowering time; basal rosette leaves spatulate or oblanceolate, 2–6 cm long and 1 cm or less wide, triple-nerved, i.e., with 1(sometimes 2) pair(s) of secondary nerves running from the base more or less parallel to the midrib, the surfaces sparsely pubescent or often glabrous, the apex rounded or obtuse and with a clear spinule, the base sheathing; principal cauline leaves linear to linear-lanceolate, (1)3–6 cm long and 2–7 mm wide, with only the midrib prominent or triple-nerved as in the basal leaves, grayish green, the indument strigose or hirsute (depending on the variety), the apex acute or obtuse and spinulose, the base rounded or slightly clasping; rameal leaves similar in contour, color, and vestiture, abruptly reduced in size, those of the peduncles bracteiform, oblong-ovate, 1.5–5(6) mm long, usually squarrose or sometimes appressed to ascending, intergrading with the phyllaries. **Capitulescence** a somewhat fastigiately branched panicle or often pyramidal at the top, the head-bearing branchlets arching, racemiform. **Flowering heads** numerous, small, mostly less than 1 cm in diameter when the rays are fully extended, crowded and secund, subsessile arising from the leaf axils, or on densely bracteate peduncles 0.5–1(2) cm long. **Involucre** cylindric or narrowly campanulate, ca 3–4 mm high, the phyllaries imbricated in 3 or 4 series. **Phyllaries** strongly graduated, firm, squarrose, with a well-delimited oblanceolate or spatulate green areole in the apical portion, the basal ¼–½ portion scarious and somewhat indurate; outer phyllaries oblanceolate to spatulate, 1.5–2 mm long, at least somewhat pubescent on both surfaces, often conspicuously scabrous-hirsute abaxially, the apex acute to obtuse and with a prominent spinule, the margins scabrous; inner phyllaries linear-lanceolate, more slender than the outer and median, 3–4 mm long, usually glabrous, acuminate or attenuate. **Receptacle** alveolate with sharp teeth. **Ray florets** 8–18(20), the corollas 4–6(7) mm long, white (rarely pink or

bluish), glabrous or with a few trichomes on the tube. **Disk florets** 8–12(15), the corollas narrowly funnelform, 2.5–4 mm long, glabrous or with a few trichomes at the throat, the limb gradually expanded, light yellow turning purple after anthesis, the lobe/limb fraction 0.3–0.35, the tube ca half as long as the limb. **Pappus** simple, the bristles about as long as the disk corolla, whitish, soft, slender, and attenuate. **Achenes** plump, oblong-obovoid, often somewhat falcate, 1.2–2 mm long and 0.4–0.6 mm across, deep purple turning brown when weathered, sericeous or densely strigillose, and with 7–9 ribs. $2n = 10$ (mostly), 20. Including *A. exiguus* Rydb. [*A. multiflorus* Aiton—Mead 1846; Brendel 1887; Higley and Raddin 1891; Pepoon 1927; Benke 1928.]

September–October. Unshaded habitats: prairie remnants, dunes, gravelly exposed slopes, and open woods; also in somewhat disturbed ground that still supports native prairie vegetation, e.g., roadsides and railroad rights-of-way, but usually not in severely weedy situations. Widely distributed throughout the state. The species range extends over much of the North American continent, in the East from s. ME to s. VA, in the Midwest from s. ON and s.e. MB to AR, and in the West from SK, AB, and e. BC through e. WA, n.e. OR, ID, and the Great Plains to NM, TX, e. AZ, and n. Mexico.

Plants of Illinois belong in subsp. *ericoides* (A.G. Jones 1978b, c), comprising var. *ericoides* and var. *prostratus* (Kuntze) S.F. Blake [*Aster exiguus*—G.N. Jones 1945, 1950, 1963; Fell 1955; Jones and Fuller 1955; Mohlenbrock and Voigt 1959]. Although these two varieties are widely sympatric and plants with intermediate characteristics have been recorded, the identity and integrity of the taxa seem to be largely maintained as follows:

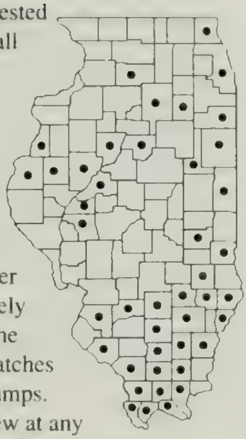
1. Pubescence of stems, leaves, and phyllaries often relatively sparse and soft, appressed-strigose, or trichomes on the stems sometimes ascending .... var. *ericoides*
1. Pubescence of stems, leaves, and phyllaries copiously and harshly hirsute, the trichomes on the stems spreading or somewhat reflexed .... var. *prostratus*

In addition, two color forms originally described from Illinois by Benke (1928, 1932b) are occasionally observed: *Aster ericoides* f. *caeruleus* (Benke) S.F. Blake (plants with blue to purplish rays), and *A. ericoides* f. *gramsii* Benke (plants with "rose-red" rays). Also included here are Illinois collections cited as belonging in the hybrid *A. ericoides* var. *prostratus* × *A. pilosus* (Mohlenbrock 1986). The hybrid formula was originally published as *A. exiguus* × *pilosus* and attributed to H.E. Ahles (Jones and Fuller 1955: 468). These plants are not hybrids but are somewhat atypical individuals of var. *prostratus*, probably the result of injury, e.g., from mowing. Hybridization is well documented and rather common between *A. ericoides* and *A. novae-angliae*. The plants are known under the binomial *A.* × *amethystinus* Nutt., pro sp. (see discussion under **14a**).

6a. *Aster falcatus* Lindley in Hooker var. ***commutatus*** (Torrey & Gray) A.G. Jones
Western Heath Aster [*A. commutatus* (Torrey & Gray) A. Gray—Fernald 1950]

A few specimens collected along a railroad track in Kane County [*Sherff 1798* (F, ILL)] seem to approach the characteristics of and perhaps belong in this taxon, which is of common occurrence from the Dakotas and Nebraska westward, especially in the Great Plains. The plants exhibit a somewhat decumbent sprawling habit, heads that are not secund and are somewhat larger than is typical for *Aster ericoides*, and an abundance of larger cauline leaves not usually present at flowering time in plants of *A. ericoides*. I have included this western taxon in the key, but if the Illinois plants really belong here, rather than representing aberrant forms of *A. ericoides* that resulted from some kind of injury or other environmental influence, they are almost certainly waifs. I do not share the view of Jones and Fuller (1955: 468), who suggested that collections of "*Aster commutatus* sensu Fernald (1950) 1433, quoad pl. Ill.—Non (Torr. & Gray) A. Gray (1884)" are hybrids between *A. ericoides* (as *A. exiguus*) and *A. pilosus*.

7. *Aster fragilis* Willd.
Brittle Aster (my suggested vernacular name), Small White Aster



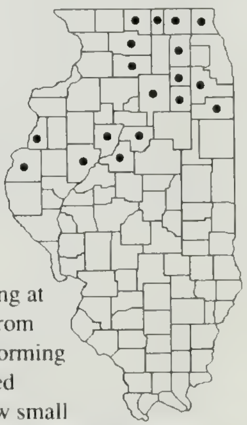
Herbaceous, with creeping (sometimes short) horizontal rhizomes. **New shoots** arising mostly from slender stoloniform rhizomes, rarely at the base of old stems, the plants forming colonial patches or scattered individual clumps. **Stems** slender, erect, 1–few at any point of emergence, 30–80(100) cm tall, commonly branched from below the middle, the branches divaricate or ascending, brittle, often slightly ridged from decurrent leaf bases, minutely puberulent in thin decurrent lines, the main stem usually glabrescent to glabrous. **Leaves** somewhat polymorphic, with clusters of smaller leaves in axils of the larger ones at most nodes, the principal leaves commonly withered and deciduous at flowering time; basal rosette leaves subpetiolate, spatulate or oblanceolate, 1–4 cm long and less than 1 cm wide, usually purple-tinged below, with several weakly expressed and anastomosing secondary nerves, glabrous, the apex acute or obtuse, the margins crenate, the subpetiolar portion sparsely ciliate, winged, and somewhat dilated toward the sheathing base; principal cauline leaves linear to linear-oblanceolate, 2–6 cm (or more) long and (1)2–3 mm wide, usually with only the midrib strongly expressed, both surfaces glabrous or the upper minutely puberulent, the apex acute to attenuate with a sharp callus point, the margins often inrolled, scabrous, entire or shallowly serrulate, the base sessile, usually slightly sheathing and decurrent; rameal leaves numerous, linear or oblong, ascending or spreading, notably unequal in size, the smaller bracteiform, those of the peduncles often aciculiform, 1–2 mm long, glabrous, intergrading with the phyllaries. **Capitulescence** a diffuse panicle, the head-bearing branchlets typically racemiform and often arching. **Flowering heads** 0.6–1 cm in diameter when the rays are fully extended, often crowded but commonly not secund, subsessile, or on slender peduncles 0.2–3 cm (or more) in length. **Involucre** 2.5–4 mm high, narrowly campanulate or turbinate, the phyllaries imbricated in 4 or 5 series. **Phyllaries** strongly graduated, appressed or the outer ones spreading, glabrous, the green areoles linear to linear-oblanceolate, usually extending over the entire length of the midrib, the apex acute, the margins sparsely ciliolate and with a scarious rim extending to near the apex; outer phyllaries slender, linear, 0.8–1 mm long; median and inner phyllaries linear-oblanceolate, the innermost 2.5–3.5 mm long, those largest in surface area (3rd or 4th series inward) typically less than twice as wide as the outer ones. **Receptacle** alveolate with sharp teeth. **Ray florets** (12)16–20, the corollas 3–4(6) mm long, white (rarely pink), glabrous. **Disk florets** 16–20 (or more), the corollas narrowly funnelform, 2.5–3.5 mm long, glabrous, the limb abruptly dilated at the throat, cream-colored or light yellow turning pink after anthesis, the lobe/limb fraction 0.35–0.45, the lobes notably recurved, the tube slightly shorter than the limb. **Pappus** simple, the bristles approximately as long as the disk corolla, whitish, soft, slender, sometimes slightly flattened at the acute apex. **Achenes** oblong-obovoid, plump or slightly compressed, 1.0–1.8 mm long and ca 0.5 mm across, gray, thinly strigillose, with 4 or 5 often obscure ribs. $2n$ = 16, 32. [*A. vimineus* misapplied, not of Lam. (cf. Jones and Hiepko 1981; Jones and Lowry 1986), including *A. vimineus* var. *subdumosus* Wieg.—Deam 1940; G.N. Jones 1950, 1963; Jones and Fuller 1955; Mohlenbrock and Voigt 1959; Gleason and Cronquist 1963; Steyermark 1963; Mohlenbrock 1975, 1986; Swink and Wilhelm 1979; and others.]

Late August–October. Moist or wet ground: bogs, meadows, lakeshores, streamsides, and open bottomlands. Occasional throughout much of the state. The range of this variable species extends from ME south to FL, and at its western limit from s. WI southward through MO and AR to LA and e. TX.

Most if not all Illinois populations belong in *Aster fragilis* var. *subdumosus* (Wieg.) A.G. Jones, a taxon typified by a collection [*Ridgway*

68 (GH)] from Olney, Richland County (Wiegand 1928: 171; A.G. Jones 1984). These plants differ from typical var. *fragilis* mainly by having relatively long peduncles, i.e., by somewhat resembling plants of *A. dumosus*. Good evidence suggests occasional hybridization and gene flow between *A. fragilis* and several other taxa that share the basic chromosome number of $x = 8$, such as *A. dumosus*, *A. lateriflorus* [e.g., *A.G. Jones 3108* (ILL) from Clark Co. and *Jelinek 221* (ILL) from Pope Co.], *A. lanceolatus* var. *interior* [e.g., *Mead s.n.* (ILL) from Hancock Co.], and *A. ontarionis* [e.g., *Shildneck 15860* (ILL) from Cass Co. and *Neill 16357* (ISM) from St. Clair Co.].

8. *Aster furcatus* Burgess in Britton & Brown
Forked Aster

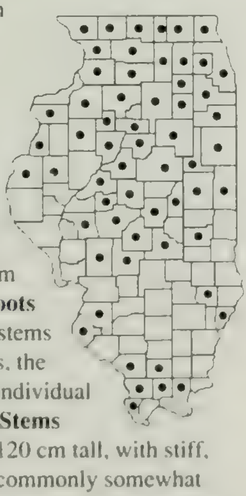


Herbaceous, with a creeping, horizontal rhizome system producing fleshy, stoloniform rhizome strands. **New shoots** arising at the base of old stems or from the rhizomes, the plants forming colonial stands or scattered individual clumps, the few small rosettes produced later in the season typically vanishing shortly after the first killing frost. **Stems** 1–several, erect, often somewhat zigzag in the upper portion, (30)50–120 cm tall, the branches typically confined to the capitulescence, ascending, more or less dichotomously forked, somewhat ridged from decurrent leaf bases, the indument uniformly distributed around the stem, hirtellous or puberulent on the upper stem and in the branches, the lower portion of the stem glabrescent. **Leaves** polymorphic, those of the basal rosettes and the main stem petiolate; leaves of new shoots and of the autumnal rosettes with oblong to ovate-lanceolate blades 4–10 cm long and 2–5 cm wide, rugose, with an often reddish midrib and several pairs of pinnate secondary nerves, minutely scabrous above and hirsute below, the apex acute or obtuse, the margins serrate, the base rounded or obliquely subcordate, the petioles short, winged, sheathing at the base; cauline leaves gradually reduced in size upward on the stem, those of the midstem with ovate to lance-ovate blades 10–12(15) cm long and (3)6–8 cm wide, rugose, with (6)8–12 pairs of pinnate secondary nerves, and with a weakly expressed reticulum of tertiary veins with more or less isodiametric areolae, harshly scabrous on the upper surface, densely hirsute over the entire lower surface resulting in a grayish green color, the apex acuminate with a long mucro, the margins sharply serrate with conspicuously mucronate teeth, the base shallowly cordate or truncate to rounded; petioles slender, mostly shorter than the blades, glabrous or irregularly ciliate, the base slightly dilated, sheathing, and somewhat decurrent; rameal leaves relatively few, similar in contour but abruptly reduced in size, subpetiolate to sessile, the base slightly clasping or sheathing, the midrib strongly keeled and decurrent; leaves of the peduncles 0–3, often bracteiform and phyllarylike, depending on the position, sometimes closely subtending the heads. **Capitulescence** variable, broad-topped, comparatively few-headed and cymiform in the natural habitat but often ample, much-branched, and compound corymbiform in disturbed situations. **Flowering heads** 2.5–3.5 cm in diameter when the rays are fully extended, not crowded and not secund, the peduncles 0.5–3(5) cm long, often leafless or nearly so, densely hirtellous or villous. **Involucre** campanulate (rarely hemispherical when pressed and dried), 6–8(10) mm high, the phyllaries imbricated in 5–7 series. **Phyllaries** appressed when fresh, strongly graduated, the outer ones ovate, 1.5–3 mm long, the innermost linear-lanceolate, 5.5–7.5 mm long, those of the outer 2 or 3 series twice as wide as the inner, puberulent on both surfaces, the apex obtuse or rounded, the margins lanate, erose-hyaline, and also often (median and inner phyllaries) with a red rim, the chlorophyllous areoles poorly delimited, with fuzzy edges, broadly obovate to rhombic or oblong, in the apical $\frac{1}{4}$–$\frac{1}{3}$ portion or rarely extending to the base in the form of bands, the basal $\frac{1}{2}$–$\frac{2}{3}$ portion scarious, indurate, and keeled or rounded on the back. **Receptacle** shallowly alveolate with blunt teeth. **Ray florets** (12)15–20, the corollas 12–18 mm long, white (sometimes aging to pink), glabrous. **Disk florets** 25–35 (or more), the corollas funnelform, 6–7(8) mm long, glabrous, the limb partway slenderly tubular, abruptly dilated 1–1.5 mm above the point of insertion of the filaments, cream-colored

or light yellow turning purple after anthesis, the fraction of lobe/expanded limb portion 0.4–0.5, the apparent tube (i.e., including the tubular limb portion) distinctly longer than the expanded limb portion. **Pappus** slightly shorter than the disk corolla, whitish or somewhat tawny, the bristles in 2 series, those of the inner series firm, with a clavellately expanded apex, those of the outer somewhat shorter, more slender, and attenuate. **Achenes** fusiform, plump, (2.5)3–3.5(4) mm long and 1–1.2 mm across, dull purple or brown, thinly puberulent in lines or glabrescent, with 8–10(12) densely spaced, often straw-colored ribs. $2n = 18$, with 0–several B-chromosomes. [*A. divaricatus* misapplied, not of L.—Mead 1846; Kibbe 1952.]

(Late July) August–October. Low springy or marshy ground in woody areas, usually underlain by sandstone or limestone: lower (mostly north-facing) slopes and edges on the cutting (eroding) sides of streams and rivers. Rare and possibly threatened, apparently less common now than is indicated by the collection records, although occasional stands are extensive. The populations are restricted to the northern one-third of the state, extending south along the major rivers to Tazewell, Fulton, and Hancock counties. The species range includes scattered stations in s. MI, w. IN, s.e. WI, e. IA, and s.e. MO.

9. *Aster laevis* L.
Smooth Aster, Smooth Blue Aster



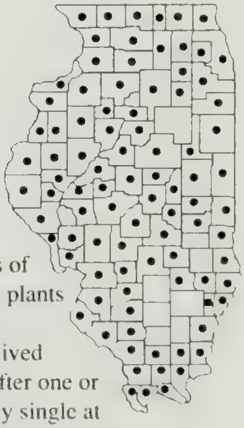
Herbaceous, with branched caudiciform or tangled rhizomes that turn woody with age but also producing stoloniform rhizome strands. **New shoots** arising at the base of old stems or from rhizome branches, the plants forming scattered individual clumps or small patches. **Stems** 1–several, erect, (30)50–120 cm tall, with stiff, typically ascending, and commonly somewhat ridged branches above the middle, often reddish in the lower portion, glaucous and essentially glabrous except for sparse hirsute indument on the peduncles and in the leaf axils. **Leaves** polymorphic, somewhat fleshy, glabrous and glaucous, the basal and larger cauline ones sometimes withered at flowering time; basal rosette leaves commonly with long, winged, and basally dilated petioles, the blades oblong or ovate to lanceolate, 3–10 cm (or more) long and ca 1–3 cm wide, the apex acute or obtuse to rounded, the margins subentire or crenate-serrate, the base rounded or truncate; principal cauline leaves subsessile or mostly sessile, extremely variable in size and shape, oblong-ovate or lanceolate to linear, sometimes abruptly constricted above the base, (4)8–15 cm long and (1)2–4.5 cm wide, with 1–several pairs of ascending secondary nerves, and a weakly expressed reticulum of tertiary veins with more or less isodiametric areolae, the apex acute or obtuse, usually callus-pointed, the margins entire or shallowly crenate-serrate, and minutely scabrous, the base often strongly auriculate-clasping; rameal leaves similar in contour but abruptly reduced in size, with a clasping or sheathing and somewhat decurrent base; leaves of the peduncles usually densely spaced, bracteiform, lance-subulate, 3–6 mm long, with an often purple callus point, intergrading with the phyllaries. **Capitulescence** a narrow or often somewhat flat-topped panicle in the upper ¼–½ of the stem, the branches commonly stiffly ascending (rarely arching). **Flowering heads** 1.5–2.5(3) cm in diameter when the rays are fully extended, terminal on somewhat ridged and often sparsely puberulent peduncles varying from 0.2 to 6 cm (or more) in length. **Involucre** campanulate, 4.5–7(8) mm high, the phyllaries imbricated in 4–6 series. **Phyllaries** strongly graduated, firm, appressed when fresh, the outer ones subulate or lanceolate, 1.5–2 mm long, the median and inner ones three times as long, linear or often slightly expanded toward the apex, the surfaces glabrous, the apical green areoles well defined, rhombic to lance-rhombic, glaucous, commonly smaller in area than the scarious basal portion, the apex obtuse, acute, or acuminate, with a sharp and often red or purple callus point, the basal portion of outer and median phyllaries usually keeled and indurate. **Receptacle** alveolate with sharp and typically bristle-tipped teeth. **Ray florets** 15–25(30), the corollas (10)12–15 mm long, blue or purple (rarely white), glabrous. **Disk florets** 15–25 (or more), the corollas narrowly funnelform, (4.5)5–6 mm

long, glabrous, the limb slightly dilated at the throat, yellow turning purple after anthesis, the lobe/limb fraction ca 0.2, the tube slightly shorter than the limb. **Pappus** simple, the bristles usually somewhat shorter than the disk corolla, tawny or rose-tinged, soft, slender, and attenuate. **Achenes** oblong-obovoid, plump or somewhat compressed, 2–3 mm long and 0.8–1.3 mm across, deep purple at maturity, or brown when weathered, glabrous, with 4 or 5 often irregularly spaced ribs. $2n = 48$.

August–October. Mesic, mostly open habitats: prairie remnants, meadows, lakeshores, stream banks, open woods, and exposed slopes; also in somewhat disturbed ground along roads and railroad rights-of-way. Fairly common throughout most of the state. The range of the species extends from PQ south to GA and AL, northwest to AB, BC, and s. YT, and in the Rocky Mts. and Great Plains southward through c. CO to NM and the Guadalupe Mts. in w. TX.

Although somewhat variable, Illinois plants are assigned to typical var. *laevis*. There is evidence of occasional hybridization and intergradation with other species that share the basic chromosome number of $x = 8$, such as *Aster lanceolatus* [e.g., *Benke 5280* (F)—cf. Benke 1932b], *A. puniceus* [e.g., *Fuller 13293a* (F) from McHenry Co.], *A. oolentangiensis* [e.g., *Heitmann & Heitmann 1027* (F) from Fulton Co.], and *A. lateriflorus* [e.g., *Benke 2927* (F) from Kane Co.].

10. *Aster lanceolatus* Willd.
Panicled Aster



Herbaceous, with a strongly creeping horizontal rhizome system. **New shoots** initiated mostly at the tips of stoloniform rhizomes, the plants extensively clonal but the connecting strands short-lived and often disintegrating after one or two seasons. **Stems** mostly single at any point of emergence, often stout, erect, 40–120(150) cm tall, pubescent in thin decurrent lines from the upper nodes, usually glabrescent or glabrous below the middle, often branching from near the base or producing in midsummer secondary shoots composed of clusters of smaller leaves plus a few heads at most of the nodes and in the leaf axils. **Leaves** polymorphic, the basal and larger cauline ones often withered or deciduous at flowering time; basal rosette leaves petiolate or subpetiolate, the blades elliptic-oblanceolate or obovate to suborbiculate, 1–8 cm long and 0.5–2 cm wide, often purplish below, with several pairs of anastomosing secondary nerves, glabrous, the apex acute, obtuse, or rounded, the margins coarsely crenate, the petioles winged and with a few long marginal cilia, the base dilated and sheathing; principal cauline leaves sessile or subsessile, elliptic or oblanceolate to linear-lanceolate, (4)6–15 cm long and (0.5)1–2(3.5) cm wide, gradually reduced in size up the stem, with relatively weakly expressed secondary nerves and a reticulum of tertiary veins with oblong areolae, glabrous (rarely scabrellous above), the apex acute to attenuate and callus-pointed, the margins sharply serrate, the base cuneate and somewhat decurrent; rameal leaves similar in contour and texture but mostly entire, those of the peduncles relatively few, flexible, 2–6(10) mm long, rarely somewhat intergrading with the phyllaries. **Capitulescence** an ample, leafy, diffuse or often narrowly elongate panicle. **Flowering heads** 1–2(2.5) cm in diameter when the rays are fully extended, rarely secund, the peduncles 0.5–5 cm in length. **Involucre** campanulate, 3.5–6(7) mm high, the phyllaries imbricated in 3–5(6) series. **Phyllaries** somewhat or often strongly graduated, comparatively slender, appressed or slightly spreading, the outer ones 1.5–3 mm long, the inner 3–6 mm; outer and median phyllaries linear-oblanceolate, glabrous on the abaxial surface, sparsely puberulent on the adaxial surface, the green areoles linear-oblanceolate, the apex acute to acuminate and callus-pointed, the margins somewhat ciliolate, erose-hyaline, and with a narrow scarious rim extending to the tip, the basal $^1/_4$–$^1/_2$ portion scarious and slightly dilated; innermost phyllaries linear, very slender, acuminate to attenuate. **Receptacle** alveolate with sharp teeth. **Ray florets** 20–35 (or more), the corollas 7–10(12) mm long, white (rarely pink),

glabrous. **Disk florets** (15)20–30 (or more), the corollas funnelform, 3–5(6) mm long, glabrous, the limb cream-colored turning purple after anthesis, dilated at the throat, with comparatively long recurved lobes, the lobe/limb fraction 0.35–0.45(0.5), the slender tube somewhat shorter than the limb. **Pappus** simple, the bristles as long as the disk corolla or often slightly longer, whitish, soft, slender, and attenuate. **Achenes** oblong-obovoid, somewhat compressed, 1.5–2 mm long and 0.5–0.8 mm across, gray, thinly strigillose, 4- or 5-ribbed. $2n = 32, 64$ (mostly), rarely 40 or 48. Including *A. simplex* Willd. and *A. interior* Wieg. (Semple 1979; Semple and Chmielewski 1987). [*A. paniculatus* Lam. non Miller; *A. tradescantii* misapplied, not of L.]

August–October. Low moist or swampy ground: woods, pastures, bottomlands of rivers and streams, ditch margins, and lakeshores. Very common. Under the broad taxonomic concept adopted by Semple and Chmielewski (1987), the species has a transcontinental range that includes localities in nearly every state and province of North America.

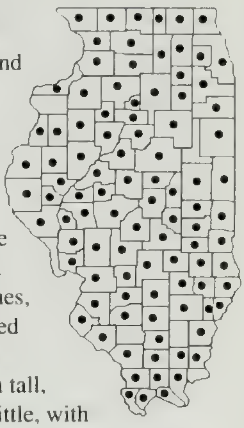
Three varieties can be distinguished in Illinois: 1) var. *lanceolatus* [*Aster paniculatus*—Brendel 1887; Higley and Raddin 1891; Pepoon 1927; Deam 1940; G.N. Jones 1945, 1950; Fell 1955. *A. simplex* var. *ramosissimus* (Torrey & Gray) Cronq.—Fernald 1950; Gleason 1952; Dobbs 1963; Gleason and Cronquist 1963; Steyermark 1963], 2) var. *simplex* (Willd.) A.G. Jones [*A. simplex* (sensu stricto)—Mead 1846; Fernald 1950; Gleason 1952; Kibbe 1952; Jones and Fuller 1955; Mohlenbrock and Voigt 1959; G.N. Jones 1963; Gleason and Cronquist 1963; Swink 1974; Mohlenbrock 1975, 1986; Swink and Wilhelm 1979. *A. paniculatus* var. *simplex* (Willd.) Burgess in Britton & Brown—Wiegand 1933; Deam 1940. *A. lanceolatus* subsp. *simplex* (Willd.) A.G. Jones—1984], and 3) var. *interior* (Wieg.) Semple & Chmielewski [*A. tradescantii* sensu auct. non L.—Mead 1846; Brendel 1887; Higley and Raddin 1891; Pepoon 1927; G.N. Jones 1950; Fell 1955. *A. vimineus* sensu auct., pro parte, non Lam.—Higley and Raddin 1891; Kibbe 1952. *A. interior*—Deam 1940; G.N. Jones 1945; Jones and Fuller 1955; Mohlenbrock and Voigt 1959. *A. simplex* var. *interior* (Wieg.) Cronq.—Fernald 1950; Gleason 1952; Gleason and Cronquist 1963; Swink 1974; Swink and Wilhelm 1979. *A.* × *interior* Wieg., pro sp.—A.G. Jones 1980a, b. *A. lanceolatus* subsp. *interior* (Wieg.) A.G. Jones—1984]. Plants of these three varieties show a great deal of intergradation. For the most part, however, they may be distinguished as follows:

1. Flowering heads 1–1.5 cm in diameter when the rays are fully extended; involucres 3–4 mm high; disk corollas 3–3.5 mm long; branchlets often racemiform ..... var. *interior*
1. Flowering heads 1.8–2.5 cm in diameter when the rays are fully extended; involucres (4)4.5–7 mm high; disk corollas typically (4)4.5–5.5 mm long; branchlets usually not racemiform.
   2. Leaves of the midstem linear-lanceolate, 12 times (or more) longer than wide .... var. *lanceolatus*
   2. Leaves of the midstem elliptic-lanceolate to oblanceolate, mostly less than 11 times longer than wide .... var. *simplex*

For a different interpretation see Semple and Chmielewski (1987). These authors do not regard *Aster simplex* as sufficiently distinct from typical *A. lanceolatus* to merit taxonomic recognition. Collections of var. *simplex* from the central and southern parts of the Midwest, however, consistently seem to differ in several ways from the more northern populations of var. *lanceolatus*. Aside from the key characters mentioned and the somewhat differential geographic distribution, plants of var. *simplex* occur more frequently in shady bottomland woods, whereas plants of both var. *lanceolatus* and var. *interior* are more common in the unshaded habitats of bogs, meadows, lakeshores, and ditch margins.

Good evidence suggests that this extremely variable species occasionally hybridizes and intergrades with other species of the $x = 8$ chromosome number assemblage, e.g., *Aster borealis*, *A. fragilis*, *A. laevis*, *A. lateriflorus*, *A. puniceus*, and others that are not elements of the flora of Illinois.

11. *Aster lateriflorus* (L.) Britton
Starved Aster, Calico Aster, Side-flowered Aster, White Woodland Aster



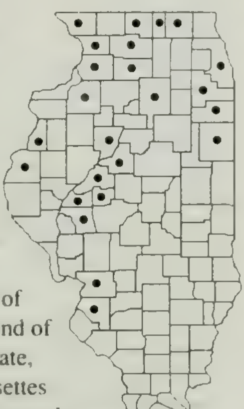
Herbaceous, with a short, somewhat tangled rhizome system. **New shoots** initiated at the base of old stems or from short ascending rhizome branches, the plants forming scattered individual clumps. **Stems** 1–several, 30–80(120) cm tall, comparatively slender, brittle, with ascending or often divaricate branches from the lower nodes resulting in a sprawling or bushy habit, the indument villous or hirtellous, usually in decurrent lines from the leaf bases, sometimes uniformly distributed in the upper branches, the main stem often glabrescent or glabrous. **Leaves** polymorphic, the larger cauline ones at least in part persistent throughout the flowering period; basal rosette leaves subpetiolate, the blades spatulate or obovate to suborbiculate, the upper surface minutely puberulent or glabrous, the lower surface villous along the midrib (rarely glabrous) and sometimes purplish, the margins crenate-serrate, abruptly narrowed to the winged, ciliate, somewhat sheathing subpetiolar base; principal cauline leaves sessile or subsessile, mostly elliptic-oblanceolate, rarely linear, (3)5–10(15) cm long and (0.2)1–2(3.5) cm wide, gradually reduced in size up the stem, usually with several pairs of anastomosing secondary nerves, and a weakly expressed reticulum of tertiary veins with oblong areolae, the upper surface typically scabrellous, the lower surface villous or hirtellous along the midrib but otherwise usually glabrous, the apex acuminate to attenuate with a sharp callus point, the margins serrate and minutely scabrous, the base cuneate and somewhat decurrent; rameal leaves similar in contour, more or less glabrous, entire, those subtending the head 1–few, oblong-lanceolate, 1.5–3 mm long, flexible, not phyllarylike. **Capitulescence** an often ample diffuse panicle, commonly branched from below the middle, the head-bearing branchlets slender and wiry, arching, racemiform. **Flowering heads** small, 0.8–1.3 cm in diameter when the rays are fully extended, often crowded, secund, sessile or subsessile, the peduncles rarely more than 1 cm in length. **Involucre** campanulate (turbinate when pressed and dried), 3.5–4.5(5) mm high, the phyllaries imbricated in (3)4 or 5 series. **Phyllaries** strongly graduated, appressed or slightly spreading, glabrous on the abaxial surface, the apical green areoles obovate-oblanceolate, the basal $^1/_3$–$^2/_3$ portion scarious except for the green midrib; outer phyllaries linear-lanceolate, 1–2 mm long, less than half as long as the inner, acute and callus-pointed; median phyllaries linear or often slightly expanded toward the acute to acuminate apex, sparsely puberulent on the adaxial surface, the margins irregularly ciliolate, erose-hyaline, and with a narrow scarious (sometimes reddish) rim extending to the tip; innermost phyllaries very slender, linear, 3.5–4.5 mm long. **Receptacle** alveolate with sharp or bluntish teeth. **Ray florets** 10–15(20), the corollas (4)5–8 mm long, white, glabrous. **Disk florets** 10–15(20), the corollas funnelform, (2.5)3.5–4.5 mm long, glabrous or with a few trichomes, the limb abruptly dilated at the throat, cream-colored or light yellow before anthesis, soon turning deep magenta, the lobe/limb fraction 0.5–0.75, the lobes strongly reflexed, the slender tube slightly shorter than the limb. **Pappus** simple, the bristles about as long as the disk corolla, white, soft, slender, and attenuate. **Achenes** oblong-obovoid, plump or slightly compressed, (1.3)1.8–2.2 mm long and 0.5–0.7 mm across, gray, sparsely strigillose, obscurely 3–5 ribbed. $2n = 16, 32$ (mostly), 48. Including *A. pendulus* Aiton, *A. horizontalis* Desf., and *A. hirsuticaulis* Lindley in DC. [*A. vimineus* Lam. (see A.G. Jones 1984: 379; Jones and Lowry 1986). *A. diffusus* Aiton—Brendel 1887; Higley and Raddin 1891. *A. miser* sensu Aiton non L.—Mead 1846.]

Late August–October. Wooded slopes, high banks of streams and rivers, and edges of bogs; Illinois plants more common in well-drained or upland situations than in wet ground habitats. Common throughout the state. The range of the species extends in the East from NB, ME, PQ, and s. ON south to FL, and to the west from MN and e. IA through e. KS to LA and s.e. TX.

Varietal names can be assigned to collections from Illinois only with the greatest difficulty because of a great deal of intergradation, not only between the varieties that have been described (Wiegand 1928) but also involving gene flow from other species with a basic chromosome number of $x = 8$, e.g., *Aster dumosus*, *A. fragilis*,

A. lanceolatus, and *A. ontarionis*. The majority of specimens more or less fit the circumscription and concept of typical var. *lateriflorus*. Plants of var. *horizontalis* (Desf.) Farw. [*A. lateriflorus* var. *pendulus* sensu Wieg. non (Aiton) Burgess in Britton & Brown] are not uncommon, especially in the southern half of the state. The characteristics that weakly distinguish this variety (very small heads combined with a sprawling habit and a tendency toward relatively moist habitats) may have been introduced in part through gene flow from *A. fragilis*. Illinois collections labelled *A. lateriflorus* var. *hirsuticaulis* (Lindley) Porter [sensu Pepoon 1927] are partly referable to *A. ontarionis* and partly to typical var. *lateriflorus*. The range of var. *hirsuticaulis* [including var. *tenuipes* Wiegand (1928)] probably does not extend to Illinois; these plants are common in the northeastern states and in Canada west to s. ON.

12. *Aster linariifolius* L.
Flax-leaved Aster,
Savory-leaved Aster



Tufted, often suffruticose, with a tangled or cormoid-caudiciform rhizome system that turns woody with age. **New shoots** arising at the base of old stems but also at the end of ascending, densely bracteate, rhizome strands; basal rosettes absent. **Stems** cespitose, several to many, slender and wiry, (10)20–40(60) cm tall, simple, or few-branched only in the capitulescence (unless injured through grazing or mowing), cinereous, puberulent, sometimes glabrescent toward the base. **Leaves** numerous, firm, densely spaced, sessile, ascending or spreading to squarrose, more or less uniform in contour, linear or nearly so, entire, those of the main stem 1.5–2.5(3.5) cm long and 1.5–2.5(4) mm wide, with a keeled midrib, the secondary venation not evident, glabrous except for the scabrous margins and the midrib below, the epidermal cells of both surfaces strikingly bulliform (hand lens needed to see this), the apex acute with a sharp callus point; lowermost cauline leaves bracteiform; rameal leaves abruptly reduced in size, those of the peduncles intergrading with the phyllaries. **Capitulescence** racemiform or corymbiform in the upper 1/6–1/4 of the stem. **Flowering heads** relatively few per stem, commonly fewer than 30, 1.5–3 cm in diameter when the rays are fully extended, on leafy peduncles 0.5–5(15) cm in length. **Involucre** turbinate or campanulate, (6)8–10(12) mm high, the phyllaries imbricated in 5–8 series. **Phyllaries** strongly graduated, firm, appressed, often largely scarious on the abaxial surface, the green areoles not well defined, centered in the apical 1/4–1/2 portion or forming two bands along the whitish midrib, sometimes extending to the base; phyllaries of the outer 2 or 3 series 2.5–4 mm long, lanceolate, notably keeled, the apex acute with a red callus point, the margins ciliate to fimbriate, or lanate toward the apex, those of the 5th or 6th series inward largest in surface area, (6)7–8(10) mm long, linear-lanceolate, keeled or rounded on the back, often with a red rim, the apex obtuse or rounded, the margins conspicuously lanate over the entire length. **Receptacle** alveolate with sharp teeth. **Ray florets** 13–17, the corollas (10)12–15(18) mm long, violet or reddish purple (rarely white), glabrous. **Disk florets** 20–30 (or more), the corollas narrowly funnelform, 5–6.5(8) mm long, glabrous, the limb gradually expanded, light yellow turning reddish after anthesis, the lobe/limb fraction ca 0.2, the tube slightly shorter than the limb. **Pappus** tawny, "double" (according to literature references) but often composed of 3 series of bristles, the principal bristles firm, in 1 or 2 series, somewhat unequal, 4–7 mm long, as long as the disk corolla or slightly shorter, with at least the innermost clavellately expanded and flattened toward the apex; bristles of the outermost whorl distinctly shorter, 1 mm long or less, and attenuate. **Achenes** obconic, plump, 2.5–3(3.5) mm long, ca 1 mm across, dull purple or brown, 3–5 ribbed, the color and sculpturing of the pericarp often obscured by densely sericeous indument. $2n = 18$. [*Diplopappus linariifolius* (L.) Hooker—Mead 1846.]

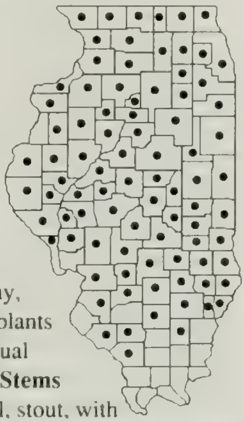
Late August–October. Dry sandy, loamy, or rocky soils: exposed slopes and ridges, open woods, dunes, and barrens. Most prominent in the northern half of the state but extending south to St. Clair County. The range of the species extends from s. PQ and ME south to FL, and to the west from MN through s. MO, s.e. KS, and e. OK to e. TX.

13. *Aster macrophyllus* L.
Large-leaved Aster,
Big-leaved Aster

Herbaceous, with a strongly creeping horizontal rhizome system. **New shoots** arising mostly at the ends of stoloniform rhizome branches, the plants typically forming extensive colonies, the autumnal basal rosettes numerous, prominent, often forming a dense ground cover. **Stems** 1–few at any point of emergence, erect, sometimes slightly zigzag in the upper portion, 30–70(90) cm tall, terete or somewhat angular above from decurrent leaf bases, often maroon-colored, the branches confined to the capitulescence, ascending, the upper stem and branches pubescent with white, multicellular, antrorsely curved or spreading trichomes and also invested with sessile or stipitate glands, the lower stem glabrescent or glabrous. **Leaves** polymorphic, those of the basal rosettes and the lower half of the stem petiolate; basal rosette leaves largest, the blades broadly ovate to cordate, (8)15–25 cm long and (6)8–12(15) cm wide, with 6–12 pairs of pinnate secondary nerves, and a reticulum of tertiary veins with more or less isodiametric areolae, the upper surface minutely scabrous or glabrous, the lower thinly puberulent, especially along the nerves, the apex acuminate with a sharp mucro, the margins crenate-serrate, each tooth mucronate, the base deeply cordate and sometimes slightly oblique, the petioles 1–2 times as long as the blades, with slightly winged and ciliate margins, dilated and sheathing at the base; cauline leaves gradually reduced in size up the stem, blades of the larger ones nearly as wide as long, similar to the basal leaves in contour and vestiture except for sparse glandularity along the midribs below, the petioles shorter and progressively more broadly winged upward on the stem; upper stem leaves subpetiolate or often sessile and clasping, ovate or obovate to oblanceolate; rameal leaves relatively few, abruptly reduced but variable in size, ovate or oval, the upper surface scabrous and stipitate-glandular, especially along the midrib and the margins, the lower surface more sparsely so, the apex acute or acuminate, the margins crenate-serrate to entire, the base rounded or cuneate, the 0–few leaves of the peduncles ovate-lanceolate, 2–5 mm long, thinly to densely glandular, attenuate, not intergrading with the phyllaries. **Capitulescence** a dichotomously branched corymbiform panicle in the upper $^{1}/_{4}$–$^{1}/_{3}$ portion of the stem, the branchlets short and firm. **Flowering heads** variable, ca 2–3 cm in diameter when the rays are fully extended, sometimes crowded in the individual cymules, the peduncles 0–2.5 cm long, often densely glandular-hirsute. **Involucre** campanulate or hemispherical, (6)8–10 mm high, the phyllaries imbricated in (4)5–7 series. **Phyllaries** appressed or somewhat spreading, strongly graduated, those of the outer 2(or 3) series ovate, 2–3 mm long and ca half as wide, acute to obtuse, the green areoles oblong-obovate, in the apical $^{1}/_{3}$–$^{1}/_{2}$ portion (rarely extending to the base in the outer phyllaries), the basal portion mostly scarious, indurate, keeled, or rounded on the back, glandular-puberulent over the entire abaxial surface (outermost phyllaries) or only in the chlorophyllous zone and along the midrib (median phyllaries), the adaxial surface more or less glabrous, the margins lanate and glandular toward the apex, hyaline toward the base, and with a scarious or often reddish rim; phyllaries of the innermost series slenderly linear-lanceolate, (6)7–9 mm long, ca 1 mm wide, acute, largely scarious or sometimes red-rimmed. **Receptacle** alveolate with sharp teeth. **Ray florets** 10–15, the corollas 10–13 mm long, varying from white to deep lavender, glabrous. **Disk florets** 20–30 (or more), the corollas funnelform, 7–8 mm long, glabrous, the limb partway slenderly tubular, more or less abruptly flared ca 1.5–2 mm above the point of insertion of the filaments, cream-colored or light yellow aging to purple, the lobes reflexed, the fraction of lobe/expanded limb portion 0.6–0.7, the apparent tube (i.e., including the tubular limb portion) much longer than the expanded limb portion. **Pappus** tawny, in 2 series of somewhat unequal bristles, those of the inner series about as long as the disk corolla, firm and with a clavellately expanded apex, those of the outer slightly shorter, more slender, and attenuate. **Achenes** slenderly fusiform or cylindric, 3.5–4(4.5) mm long and 1–1.2 mm across, dull purple or brown, glabrous or with a few scattered trichomes near the top, with 8–10 thick, densely spaced (sometimes double-stranded), glossy, golden-brown ribs. $2n = 72$.

August–October. Moist or swampy ground (sometimes dry soil) in wooded areas. Local, rare in this state, recorded only from Cook and Lake counties, much more common to the north and east of Illinois. The range of this variable species extends in the East from NS, PE, NB, and PQ south to GA, in the Midwest from ON south to s.e. IN, and at the western limit from e. MB through e. MN to n.e. IA.

14. ***Aster novae-angliae*** L.
New England Aster



Herbaceous, with a tangled or sometimes caudiciform rhizome system. **New shoots** arising at the base of old stems or from short, fleshy, horizontal rhizomes, the plants forming scattered individual clumps or small patches. **Stems** 1–several, 50–150 cm tall, stout, with ascending or divaricate branches from above the middle, densely hispidulous-hirsute or pilose, stipitate-glandular in the upper portion, the lower portion less pubescent and usually brown in color. **Leaves** numerous, polymorphic, the basal and lower cauline ones often withered and deciduous at flowering time; basal rosette leaves spatulate, ca 2–6 cm long and 0.5–1.5 cm wide, with 1–3 pairs of anastomosing secondary nerves more or less aligned with the midrib or margins, sparsely hirsute on both surfaces, the margins ciliolate and occasionally with a few shallow teeth; principal cauline leaves sessile and entire, oblong or lanceolate, with several pairs of weakly expressed secondary nerves, and a reticulum of tertiary veins with more or less isodiametric areolae; leaves of the midstem ca 5–10 cm long and 5–15(20) mm wide, thinly strigose above, hirsute or hispidulous below, and invested with both sessile and stipitate glands (more copiously so in the upper leaves), the apex acute and mucronulate, the margins pustulate-scabrous, the base auriculate-clasping; rameal leaves similar in contour and vestiture, gradually reduced in size, the 1–4 small leaves of the peduncles not phyllarylike. **Capitulescence** a leafy, broad, round-topped or somewhat corymbiform panicle in the terminal $(^1/_{10})^1/_6$–$^1/_3$ portion of the stem. **Flowering heads** 2–4.5(5) cm in diameter when the rays are fully extended, often crowded but not secund, the peduncles 0.3–4 cm long, glandular and hispidulous, commonly somewhat dilated just below the head. **Involucre** broadly hemispherical, 5–15 mm high, the numerous phyllaries imbricated in 4–6 series. **Phyllaries** slender, linear-lanceolate, long-acuminate or attenuate, commonly strongly squarrose or reflexed, mostly subequal in length, (5)6–12(15) mm long or the outer ones slightly shorter (rarely longer) than the inner; outer phyllaries largely herbaceous, dark green and often purple-tinged, densely invested with both stipitate and sessile glands; median and inner phyllaries scarious in the basal $^1/_3$–$^1/_2$ portion. **Receptacle** shallowly alveolate or merely pitted. **Ray florets** numerous, ca 50–100, the corollas 10–20(25) mm long, rose-colored to deep purple (rarely white), with a few trichomes near the throat. **Disk** 5–15 mm in diameter. **Disk florets** numerous, 50 or more, the corollas narrowly funnelform, (4)5–7 mm long, thinly puberulent in the throat region, the limb only slightly expanded, light yellow turning purple after anthesis at least in the lobes, the lobe/limb fraction 0.2–0.25, the tube ca half as long as the limb. **Pappus** simple, the bristles somewhat unequal and often slightly shorter than the disk corolla, tawny or rose-tinged, soft, slender, and attenuate. **Achenes** oblong to obconic, plump, 1.8–2.5(3) mm long, ca 0.6–1 mm across, dull purple or brown, obscurely glandular and densely sericeous, with 7–9 ribs. $2n = 10, 20$, occasionally with supernumerary chromosomes.

August–October. Unshaded mesic situations: prairie remnants, open woods, streamsides, fens, also in disturbed soils of pastures, old fields, roadsides, and railroad rights-of-way. Common throughout the state; also widely cultivated and often escaped, a fact that partly accounts for the various color forms observed. The range extends from s. PQ, s. ON, and ME south to AL, MS, and AR, west to s. MB, c. ND, c. NE, and e. KS, with scattered stations in WY, CO, OK, and NM.

Including f. *roseus* (Desf.) Britton [var. *roseus* (Desf.) DC.—Higley and Raddin 1891; Pepoon 1927; Benke 1928], plants with rose-colored rays; and f. *geneseensis* House (Benke 1932a), a white-rayed form. A short-lived, large-headed, white-rayed individual found in Champaign County (*A.G. Jones 2604*), to which

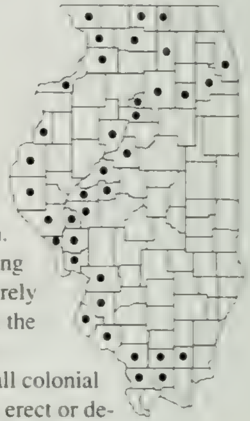
I have applied the latter name, possessed an extra set (genome) of chromosomes (A.G. Jones 1980b). When cross-pollinated from a typical individual, a few viable achenes were produced that grew into typical purple-rayed plants. Hybrids between plants of *Aster novae-angliae* and *A. ericoides* [*A.* × *amethystinus*] are occasionally found in Illinois (see **14a**).

14a. ***Aster* × *amethystinus*** Nutt., pro sp.
[*A. ericoides* × *A. novae-angliae*]

This hybrid is readily identifiable (Benke 1930) and has also been produced experimentally (Wetmore and Delisle 1939; A.G. Jones 1978c). The plants occur with sufficient frequency in Illinois to warrant inclusion in the key and a comparative diagnosis: **Habit** similar to that of *Aster novae-angliae*, the plants usually with a tangled rhizome system and short stoloniform strands forming small patches. **Stems** erect, aging to a light brown color, densely hispidulous-hirsute but not glandular. **Leaves** numerous, sessile, at least some of the larger cauline ones persistent throughout the flowering period and with clusters of smaller leaves produced in the axils; principal cauline leaves linear or oblong to elliptic-oblanceolate, 4–6 cm long and 3–6 mm wide, copiously and harshly hirsute on both surfaces but not glandular, the apex acute or obtuse, mucronulate, the margins entire and scabrous, the base rounded or slightly clasping but not auriculate; rameal leaves similar in contour and vestiture, those of the peduncles few, oblong-lanceolate, 3–5 mm long, not intergrading with the phyllaries. **Capitulescence** an ample leafy panicle with ascending branches and a pyramidal or round top. **Flowering heads** intermediate to the two parent species in most characteristics, 1.3–2 cm in diameter when the rays are fully extended, often crowded, sometimes secund. **Involucre** hemispherical, 4–6 mm high. **Phyllaries** strongly reflexed, somewhat graduated or often subequal, scabrous-puberulent but not glandular, mostly with a conspicuous, scarious basal portion. **Ray florets** 20–30 (or more), the corollas 5–10 mm long, lavender. **Disk** 4–7(8) mm in diameter. **Disk florets** 20–30 (or more), the corollas 3–4 mm long. **Pappus** tawny or rose-tinged. **Achenes** fusiform or obconic, 1.5–2 mm long, dull purple or brown, densely sericeous but not glandular, 7–9 ribbed. $2n = 10$.

Collections of this hybrid have been recorded in habitats shared with the parental species from Champaign, Cook, De Witt, Du Page, Fulton, McHenry, Menard, Peoria, Piatt, Richland, Vermilion, and Winnebago counties. The specimens show considerable variability and are probably not all first generation hybrids.

15. ***Aster oblongifolius*** Nutt.
Aromatic Aster



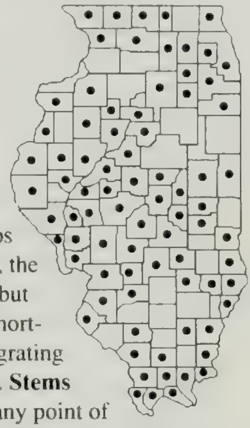
Herbaceous, with a tangled, often stoloniform or sometimes caudiciform rhizome system. **New shoots** usually arising from rhizome strands (rarely at the base of old stems), the plants forming scattered sprawling clumps or small colonial stands. **Stems** 1–several, erect or decumbent, brittle, 15–70(100) cm tall, with ascending or divaricate branches from below the middle, variably hispidulous-hirsute or hirtellous and also glandular, more copiously so on the branches, the lower stem usually lacking glands. **Leaves** numerous, at least some of the larger cauline ones persistent throughout the flowering period; basal rosette leaves oblanceolate or spatulate, 2–5(7) cm long and 0.5–1.5 cm wide, with 1–3 pairs of secondary nerves aligned with the midrib or the margins, hirsute, often also glandular (rarely glabrous or nearly so), the apex rounded and with a short mucro, the margins entire and coarsely ciliate (sometimes remotely toothed); principal leaves sessile, oblong or linear-lanceolate, (1.5)3–10 cm long and 0.5–1.5(2) cm wide, usually with 1–3 pairs of weakly expressed and anastomosing secondary nerves, and a reticulum of tertiary veins with more or less isodiametric areolae, the upper surface usually scabrous and often glandular, the lower copiously hirsute, the apex acute or obtuse, spinulose-mucronulate, the margins entire and scabrous-ciliolate, the base rounded or slightly clasping but not auriculate, often with axillary clusters of smaller leaves; upper cauline and rameal leaves gradually reduced in size, similar in contour, copiously invested with both sessile

and stipitate glands; leaves of the peduncles bracteiform, densely spaced, several to many, linear or oblong, 3–8 mm long, spinulose, usually spreading or squarrose, rarely ascending, more or less intergrading with the phyllaries. **Capitulescence** an often ample, leafy, diffuse panicle commonly branching from the lower nodes. **Flowering heads** 1.5–3 cm in diameter when the rays are fully extended, usually not secund, on glandular-hispidulous peduncles 0.5–5 cm in length. **Involucre** campanulate (or hemispherical when pressed and dried), 5–7(8) mm high, imbricated in 4–6 series. **Phyllaries** not strongly graduated, sometimes subequal, 3.5–7(8) mm long, densely glandular on both surfaces and along the margins, those of the outer 2 or 3 series with strongly squarrose tips; outermost phyllaries sometimes largely herbaceous, oblanceolate, acute; median phyllaries green in the apical $\frac{1}{3}$–$\frac{1}{2}$ portion, linear-lanceolate, long-acuminate or attenuate, the margins erose-hyaline or ciliolate, the basal $\frac{1}{2}$–$\frac{2}{3}$ portion scarious; innermost phyllaries very slender. **Receptacle** alveolate with sharp teeth. **Ray florets** (20)25–35, the corollas lavender to deep purple (rarely white), 10–15 mm long, glabrous or nearly so. **Disk florets** 30–40 (or more), the corollas narrowly funnelform to nearly tubular, 4.5–6 mm long, glabrous or nearly so, the limb weakly delimited, deep yellow before anthesis aging to reddish purple, the lobe/limb fraction 0.18–0.2, the tube ca half as long as the limb. **Pappus** simple, the bristles somewhat shorter than the disk corolla, tawny or commonly rose-tinged, soft, slender, and attenuate. **Achenes** fusiform or obovoid, often slightly falcate, 2–2.5 mm long, 0.5–0.8 mm across, dull purple at maturity or brown when weathered, strigillose or sericeous, with 7–10(11) straw-colored ribs. $2n = 10, 20$.

Late August–October. Dry sandy, loamy, or rocky soils in mostly open habitats: dunes, hill prairies, open-wooded bluffs, and sandstone or calcareous cliffs. Locally abundant in uplands associated with larger rivers. The range of the species extends from PA south to AL, west to w. ND, s.c. CO, n.c. NM, and n.c. TX.

Most if not all the plants in Illinois belong in typical var. *oblongifolius* [including *Aster oblongifolius* var. *angustatus* Shinners (1941)—Gleason 1952; Gleason and Cronquist 1963; Steyermark 1963]. Occasional plants seem to verge toward the southwestern var. *rigidulus* A. Gray [*A. Kumleini* (sic) Fries ex A. Gray (1884), pro syn.], which is distinct by being comparatively low-stemmed with numerous firm, relatively small leaves and by having a notably fastigiate branching habit.

16. *Aster ontarionis* Wieg.
Ontario Aster



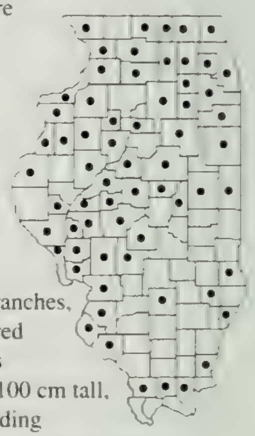
Herbaceous, with a creeping horizontal rhizome system. **New shoots** initiated at the tips of stoloniform rhizomes, the plants forming colonies but the connecting strands short-lived and mostly disintegrating after one or two seasons. **Stems** single (rarely 2 or 3) at any point of emergence, 40–120 cm tall, erect, with ascending or divaricate branches from near or below the middle and also in midsummer with short secondary shoots composed of smaller leaves plus a few heads arising from the leaf axils, the indument villous or hirsute, uniformly distributed on the branches, often in decurrent lines in the middle portion of the stem, the lower portion glabrescent. **Leaves** polymorphic; vernal rosette leaves with spatulate to oblanceolate-obovate blades, sometimes purplish below, minutely puberulent or rarely glabrous on both surfaces, the apex acute to rounded, the margins crenate-serrate, abruptly narrowed to a winged, ciliate, somewhat sheathing subpetiolar base; principal cauline leaves usually persistent throughout the flowering period, sessile or subsessile, oblanceolate or elliptic-lanceolate, 2–8(12) cm long and 0.5–3.5 cm wide, gradually reduced in size upward on the stem, with several pairs of anastomosing secondary nerves, and with a weakly expressed reticulum of tertiary veins with oblong areolae, scabrellous above, softly (often minutely) puberulent over the entire lower surface, and sometimes densely villous along the midrib below, the apex acute or acuminate to short-attenuate, usually callus-pointed, the margins crenate-serrate and ciliolate, the base cuneate and somewhat decurrent; rameal leaves similar in contour and vestiture but entire and notably unequal in size, those subtending the

head 1–few, linear-lanceolate, 1–3 mm long, flexible, not phyllarylike. **Capitulescence** an often ample, diffuse or elongate panicle above the middle of the stem, the head-bearing branchlets ascending or spreading but not strongly arching and typically not racemiform. **Flowering heads** 0.8–1.5 cm in diameter when the rays are fully extended, often crowded but typically not secund, subsessile or on peduncles 0.2–1(2) cm in length. **Involucre** campanulate (turbinate when pressed and dried), 3–4.5(5) mm high, the phyllaries imbricated in 3–5 series. **Phyllaries** appressed or somewhat spreading, strongly graduated, the outer ones 1–2 mm long, less than half as long as the inner, slenderly linear, the median ones somewhat expanded toward the tip, the green areoles linear-oblanceolate, often extending to the base, both surfaces slightly puberulent, the apex acute or acuminate and callus-pointed, the margins irregularly ciliolate, hyaline, and with a scarious rim extending to the tip; innermost phyllaries glabrous, very slender and attenuate. **Receptacle** alveolate with sharp teeth. **Ray florets** 15–25, the corollas 4–8 mm long, white, glabrous or nearly so. **Disk florets** 12–20 (or more), the corollas funnelform, (2.5)3–4.5 mm long, glabrous, the limb strongly flared, cream-colored or light yellow before anthesis turning magenta or purple, the lobes long and reflexed, the lobe/limb fraction 0.5–0.6, the slender tube slightly shorter than the limb. **Pappus** simple, the bristles about as long as the disk corolla whitish, soft, slender, and attenuate. **Achenes** oblong-obovoid, plump or slightly compressed, 1.2–1.8(2) mm long, 0.4–0.6 mm across, gray, strigillose, and often puncticulate (caused by the pustulate trichome bases), with 3–5 ribs. $2n = 32$. [*A. missouriensis* Britton in Britton & Brown non (Nutt.) Kuntze, including var. *thyrsoides* (A. Gray) Wieg.—Deam 1940. *A. lateriflorus* var. *hirsuticaulis* misapplied, not of (Lindley) Porter—Pepoon 1927, at least in part. *A. pantotrichus* S.F. Blake (see Shinners 1949)—G.N. Jones 1945.]

September–October. Moist ground habitats: river bottoms, creek margins, bogs, and marshes, frequently in wooded areas. Common throughout the state. The species range extends in the East from s.w. PQ, s.w. ON, and NY south to AL, and at the western limit from MN and n.e. SD through e. NE and s.e. KS to e. TX and n. LA.

Some of the specimens examined suggest intergradation with other species that share the basic chromosome number of $x = 8$, e.g., *Aster fragilis*, *A. lanceolatus*, and *A. lateriflorus*. A considerable number of herbarium specimens have been misidentified as *A. lateriflorus*. If rhizomes are lacking, the two species are sometimes not readily distinguishable.

17. *Aster oolentangiensis* Riddell
Sky-blue Aster, Azure Aster



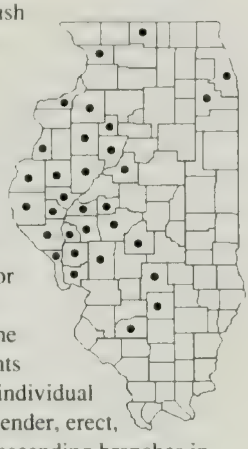
Herbaceous, with short horizontal rhizomes or a branched-caudiciform system. **New shoots** arising at the base of old stems or from rhizome branches, the plants forming scattered individual clumps. **Stems** 1–several, erect, (30)60–100 cm tall, typically with stiff, ascending branches above the middle, nearly glabrous or with hispidulous lines in the leaf axils and along decurrent leaf bases, the head-bearing branchlets slightly ridged, often uniformly scabrous-puberulent. **Leaves** polymorphic, the basal and lower cauline ones petiolate, commonly persistent throughout the flowering period; blades of basal rosette and larger cauline leaves ovate to ovate-lanceolate, 4–15(18) cm long and 1–4(6) cm wide, with 2–several pairs of anastomosing secondary nerves, and a reticulum of tertiary veins with more or less isodiametric areolae, the upper surface scabrous, the lower softly hirsute, the apex acute to acuminate, the margins subentire to shallowly serrate, the base rounded, cordate, or truncate, the petioles twice as long (or more) as the blades, slightly winged, ciliate, dilated toward the sheathing base; leaves of the midstem subpetiolate or sessile, ovate-lanceolate (in Illinois plants), gradually or somewhat abruptly reduced, acute or attenuate, and callus-pointed, the margins entire and scabrous, the base cuneate and somewhat decurrent; rameal leaves abruptly reduced in size, linear-lanceolate or subulate, appressed or closely ascending, those of the peduncles bracteiform, densely spaced, 1.5–3(4) mm long, scabrous-margined, intergrading with the phyllaries. **Capitulescence** typically a narrow thyrsiform panicle in the upper

$^1/_4$–$^1/_2$ portion of the stem, the branches ascending, sometimes racemiform. **Flowering heads** 1.5–2 cm in diameter when the rays are fully extended, sometimes secund, the peduncles variable in length to 6 cm, densely bracteate. **Involucre** cylindric to campanulate (often turbinate when pressed and dried), 5–7 mm high, the phyllaries imbricated in 4 or 5(6) series. **Phyllaries** strongly graduated, appressed or those of the outer series slightly spreading, glabrous, the outer ones 1.5–2 mm long, less than half as long as the inner, linear-lanceolate to subulate, the median and inner ones linear or often slightly expanded toward the apex, the apical green areoles rhombic, usually shorter than the indurate, scarious basal portion of the phyllaries, the apex sharply acute, acuminate, or obtuse, and mucronulate, the margins erose-hyaline and somewhat ciliolate. **Receptacle** alveolate with sharp teeth. **Ray florets** (12)15–20, the corollas 8–12(14) mm long, commonly blue or violet-purple (rarely white), glabrous. **Disk florets** 15–25 (or more), the corollas narrowly funnelform, 4–4.5 mm long, glabrous, the limb light yellow turning deep purple after anthesis, the lobe/limb fraction 0.2–0.25, the tube considerably shorter than the limb. **Pappus** simple, the bristles about as long as the disk corolla, cream-colored or slightly rose-tinged, soft, slender, and attenuate. **Achenes** oblong-obovoid, somewhat compressed, 1.8–2 mm long and less than 1 mm across, dull purple, or straw-colored with purple streaks, glabrous or nearly so, with 4 or 5 ribs. $2n = 32$; reported chromosome counts of $2n = 36$ (under the name *A. azureus*) are probably in error (A. G. Jones 1977). [*A. azureus* Lindley in Hooker—most authors prior to this publication (see A.G. Jones 1983).]

August–October. Dry sandy, loamy, or rocky soils in relatively open or unshaded situations: prairie remnants, open woods, bluffs, dunes, and barrens. Locally common throughout the state. The species range extends from s. ON and w. NY west to MN and e. SD and south through the central states to n.c. FL, LA, and n. TX.

Plants in Illinois belong in typical var. *oolentangiensis* (cf. A.G. Jones 1983). There is some suggestion of intergradation with and gene flow from other species that share the basic chromosome number of $x = 8$, e.g., *Aster drummondii* and *A. laevis*.

18. ***Aster parviceps*** (Burgess in Britton & Brown) Mack. & Bush
Small-headed Aster



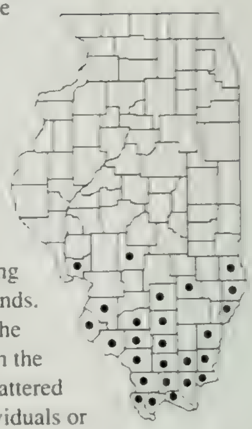
Short-lived herbaceous perennial with a caudiciform rhizome. **New shoots** originating at the base of old stems or often from root sprouts produced in autumn of the previous season, the plants forming small scattered individual clumps. **Stems** 1–few, slender, erect, 20–70(90) cm tall, with ascending branches in the upper $^1/_3$–$^1/_2$ portion, variably pilose to hirsute, the indument uniformly distributed or sometimes in decurrent lines from the leaf bases, the lower stem glabrescent. **Leaves** polymorphic, the basal and larger ones commonly withered and deciduous at flowering time; basal rosette leaves subpetiolate, oblanceolate or spatulate, 1–4 cm long and 3–7 mm wide, with weakly expressed anastomosing secondary nerves, glabrous or sparsely pubescent, and often purplish on the lower surface, the apex obtuse and bristle-tipped, the base sheathing; cauline leaves sessile, often with clusters of smaller leaves in the axils, those of the midstem linear-oblanceolate to lanceolate, 4–8 cm long and 2–5 mm wide, thinly pilose above, puberulent to hirsute below or sometimes nearly glabrous, the apex acute to attenuate and usually armed with a hyaline bristle, the margins entire or shallowly serrate, ciliolate; rameal leaves copious, mostly subulate and spinulose, those of the peduncles bracteiform, appressed or ascending, 2–4 mm long, scabrous-margined, intergrading with the phyllaries. **Capitulescence** a narrow panicle, with a pyramidal or flat top, in the upper $^1/_4$–$^1/_2$ portion of the stem, the branches ascending or sometimes arching, typically racemiform. **Flowering heads** small, 7–10 mm in diameter when the rays are fully extended, secund, the peduncles densely bracteate, 0.3–2(4) cm long. **Involucre** cylindric to narrowly campanulate (turbinate when pressed and dried), 3–4.5 mm high, the phyllaries imbricated in 3–5 series. **Phyllaries** graduated, appressed when fresh, glabrous, the apical green areoles lance-rhombic; outer phyllaries subulate, 1.5–2 mm long, ca half

as long as the inner; median and inner phyllaries linear-lanceolate, attenuate or acuminate with marginally inrolled spinulose tips, the margins erose-hyaline and commonly slightly ciliolate, the basal $\frac{1}{2}$–$\frac{3}{4}$ portion scarious. **Receptacle** alveolate with sharp teeth. **Ray florets** 10–16(18), the corollas ca 5 mm long, white, glabrous. **Disk florets** 8–10(15), the corollas narrowly funnelform, (2)2.5–3 mm long, glabrous, the limb light yellow turning purple after anthesis, the lobe/limb fraction 0.25, the tube shorter than the limb. **Pappus** simple, the bristles about as long as the disk corolla, white, soft, slender, and attenuate. **Achenes** oblong, plump, 0.8–1.5 mm long and 0.4–0.6 mm across, whitish or gray, puberulent, obscurely 2–4 ribbed. $2n$ = 16, 32. [*A. tenuifolius* misapplied, not of L.—Mead 1846. *A. pilosus* Willd. subsp. *parviceps* (Burgess in Britton & Brown) A.G. Jones (1984).]

August–October. Sandy or loamy soils in mostly unshaded habitats: barrens, hill prairies, rarely in somewhat disturbed ground that still supports prairie vegetation. Not common; mostly occurring in the western half of the state but also recorded from Cook and Will counties. As delimited herein [i.e., not including *Aster depauperatus* (Porter) Fern.], the species range extends from IA and IL south to MO, n. AR, and s.e. KS, with one station recorded from n.e. OK.

Aster parviceps is very closely related to *A. pilosus* and was originally described as a variety of that species (under the name *A. ericoides parviceps* Burgess in Britton & Brown). For the time being and pending further study, I have reversed my decision (1984) to combine the two species, mainly because their habitats and reproductive vigor are strikingly different. Furthermore, there seems to be a difference in the predominant ploidy levels. Based on x = 8 chromosomes, plants of *A. parviceps* are recorded as being mostly diploid or sometimes tetraploid (Semple and Chmielewski 1985), whereas those of *A. pilosus* are generally hexaploid, at least in my experience.

19. *Aster patens* Aiton
Spreading Aster, Late Purple Aster



Herbaceous, with a branched-caudiciform, often tangled or sometimes cormoid rhizome system, but also producing stoloniform rhizome strands. **New shoots** initiated at the base of old stems or from the rhizomes, resulting in scattered 1–several stemmed individuals or small patches. **Stems** erect, brittle, often stout, 50–100(120) cm tall, with stiff divaricate or ascending branches above the middle, the indument uniformly distributed around the stem, variously scabrous-hirsute to cinereous-puberulent, or villous on the branches and peduncles. **Leaves** polymorphic, the basal and lower cauline ones withered and deciduous at flowering time; basal rosette leaves spatulate, rugose, with 1–4 pairs of arching and anastomosing secondary nerves, variously scabrous-hirsute, the apex acute to rounded, the margins entire or often with a few teeth, the narrowed subpetiolar base winged and sheathing; principal cauline leaves ovate-lanceolate to oblanceolate, rarely spatulate, often constricted above the strongly auriculate-clasping base, 2–6(10) cm long and 1–2(2.5) cm wide, grayish green, rugulose on both surfaces, with usually pinnate and anastomosing secondary nerves, and a reticulum of tertiary veins with isodiametric areolae, variously pubescent, more densely so along the midrib below, the apex acute or obtuse and with a short mucro, the margins entire or appearing minutely denticulate from the pulvinate bases of coarse scabrous cilia; rameal leaves abruptly reduced in size, those of the peduncles bracteiform, 1–3(5) mm long, appressed or sometimes squarrose, intergrading with the phyllaries. **Capitulescence** an open, divaricately branched panicle. **Flowering heads** 2–3.5 cm in diameter when the rays are fully extended, not crowded and not secund, typically at the ends of stiffly ascending or spreading, densely bracteate peduncles 2–10(15) cm in length. **Involucre** campanulate to turbinate, 5–8(10) mm high, the phyllaries imbricated in

5–8 series. **Phyllaries** strongly graduated, linear to ovate-lanceolate, appressed or often slightly recurved-spreading, strigillose or cinereous-puberulent on the abaxial surface and near the tip on the adaxial surface, the apical portion also frequently invested with both sessile and short-stipitate glands; outer phyllaries 1.5–2.5 mm, the inner (4)6–7 mm long; median phyllaries acute or acuminate to obtuse, the chlorophyllous areoles grayish green, rhombic-oblanceolate, poorly delimited in the apical ($^1/_4$)$^1/_3$–$^1/_2$ portion, mostly shorter than the scarious basal portion. **Receptacle** shallowly alveolate with sharp or rounded teeth. **Ray florets** (12)15–25 (or more), the corollas typically blue or deep purple (rarely white), 10–15(17) mm long, glabrous or with a few scattered trichomes. **Disk florets** 20–50, the corollas narrowly funnelform, 4.5–6 mm long, glabrous or nearly so, the limb light yellow turning purple after anthesis, the lobe/limb fraction 0.18–0.2, the tube shorter than the limb. **Pappus** simple, the bristles about as long as the disk corolla or slightly shorter, tawny, soft, and attenuate. **Achenes** oblong-obovoid or fusiform, plump, 2.5–3.5 mm long and 0.8–1.2 mm across, dull purple or brown, sericeous or strigillose, with 7–10 ribs. $2n$ = 10, 20 (Illinois plants). Including *A. patentissimus* Lindley in Hooker (see R.L. Jones 1983).

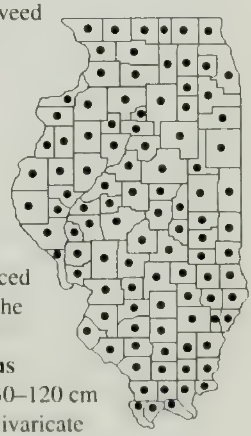
September–October. Dry sandy or rocky soils: edges of Ozarkian forest lands, open-wooded bluffs, sandstone and limestone ridges; also in disturbed soils of clearings and old fields. Occasional in the southern one-third of the state, north to Jersey, Montgomery, and Crawford counties. The range of the species extends from New England to n. FL, west to s. IL, s. and c. MO, s.e. KS, and the eastern half of OK and TX.

Two sympatric varieties have been recorded from Illinois with approximately equal frequency, var. *patens* and var. *patentissimus* (Lindley in Hooker) Torrey & Gray. The taxa intergrade freely but may be distinguished as follows:

1. Involucre 8–10 mm high, broadly campanulate or turbinate; median phyllaries ovate-lanceolate, 1.2–1.5 mm in width, obtuse, appressed, copiously cinereous-strigillose on the back, not conspicuously glandular, or toward the apex with minute sessile glands that are obscured by the indument .... var. *patentissimus*
1. Involucre usually less than 8 mm high, slenderly campanulate or turbinate; median phyllaries linear-lanceolate, mostly less than 1.2 mm in width, acute or acuminate, somewhat recurved-spreading, sparsely strigillose on the back mainly along the midrib, conspicuously glandular with both sessile and short-stipitate glands .... var. *patens*

The var. *patentissimus* was originally described (as *Aster patentissimus*) from a Missouri collection and is, according to Steyermark (1963), the more common form of *A. patens* in the Ozarks. Plants of typical var. *patens* are more prevalent to the east. Occasional herbarium collections seem to verge morphologically toward the small-leaved and slender-stemmed southern var. *gracilis* Hooker. However, plants of the latter variety are largely diploid [$2n$ (= $2x$) = 10], and that ploidy level has not been recorded for Illinois collections (A.G. Jones 1980b; R.L. Jones 1983). Specimens forming the basis for records from the Chicago region (Higley and Raddin 1891; Pepoon 1927), including *A. patens* [var.] *phlogifolius* sensu Higley &Raddin and Pepoon non (Muhl. ex Willd.) Nees, do not belong in this species.

20. *Aster pilosus* Willd.
Hairy Aster, Frost-weed Aster



Herbaceous, with a caudiciform rhizome. **New shoots** arising at the base of old stems or from root sprouts produced in the previous season, the plants forming scattered individual clumps. **Stems** 1–several, stout, erect, 30–120 cm tall, with ascending or divaricate branches from near or below the middle, variously pilose to hirsute, the indument in decurrent lines from the nodes or often uniformly distributed, sometimes the stems glabrous or nearly so. **Leaves** polymorphic, the basal and larger cauline ones commonly withered and deciduous at flowering time; rosette leaves

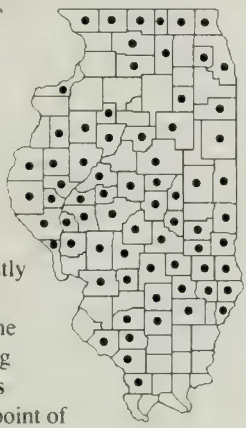
spatulate, the blade 1–6 cm long and 0.5–1.5 cm wide, abruptly narrowed to a winged subpetiolar portion, with 1 or 2 pairs of secondary nerves arching toward the apex, glabrous, or the lower surface thinly pilose along the midrib and often purplish, the apex rounded or obtuse, the margins softly ciliate or scabrous and often shallowly serrate, the base sheathing; cauline leaves sessile or subsessile, often with clusters of smaller leaves in the axils, the principal ones elliptic-oblanceolate to linear-lanceolate, 4–12 cm long and 0.5–2.5 cm wide, gradually reduced in size upward on the stem, with a prominent midrib and 1–several pairs of anastomosing secondary nerves, glabrous to variously pilose or hirsute (more so along the nerves below), the apex attenuate and usually armed with a hyaline spinule, the margins serrate or often entire, softly ciliate, the base cuneate, somewhat sheathing and decurrent; rameal leaves copious, subulate, those of the peduncles bracteiform, often densely spaced, appressed to ascending or sometimes spreading, 3–6(10) mm long, ciliolate, more or less intergrading with the phyllaries. **Capitulescence** an ample, leafy, usually diffuse panicle, the branches commonly racemiform. **Flowering heads** 1.5–2(2.5) cm in diameter when the rays are fully extended, often crowded and secund, subsessile, or on densely bracteate peduncles 0.5–3(5) cm in length. **Involucre** campanulate or broadly urceolate (i.e., somewhat constricted below the slightly recurved phyllary tips), 3.5–5(6) mm high, the phyllaries imbricated in 4 or 5 series. **Phyllaries** commonly at least somewhat graduated (rarely subequal in length), appressed or slightly spreading, glabrous except for a few marginal cilia near the apex; outer phyllaries subulate, 2–3(4) mm long, sometimes largely herbaceous, the median and inner ones linear-oblanceolate, 3–5(5.5) mm long, with broadly rhombic to lance-rhombic green areoles in the apical $^1/_4$–$^1/_2$ portion, the scarious basal portion somewhat indurate and rounded on the back, the apex with sharply acute or marginally inrolled acuminate tips, spinulose, the margins erose-hyaline. **Receptacle** shallowly alveolate with sharp teeth. **Ray florets** 15–30, the corollas 7–9(10) mm long, white (rarely pink), glabrous. **Disk florets** 30–40 (or more), the corollas narrowly funnelform, (3)3.5–4.5 mm long, glabrous or nearly so, the limb cream-colored or light yellow turning lavender or reddish purple after anthesis, the lobe/limb fraction 0.25–0.3, the tube much shorter than the limb. **Pappus** simple, the bristles about as long as the disk corolla, white, soft, slender, and attenuate. **Achenes** oblong, plump, 1–1.5 mm long and 0.5–0.7 mm across, whitish or gray, minutely puberulent, and obscurely 2–4 ribbed. $2n$ = 32, 40 (rarely), 48 (mostly). Including *A. pringlei* (A. Gray) Britton in Britton & Brown. [*A. ericoides* misapplied, not of L.—Brendel 1887; Higley and Raddin 1891; Pepoon 1927; Benke 1928; Kibbe 1952, in part. *A. villosus* Michaux non Thunb. *A. ericoides* var. *villosus* (Michaux) Torrey & Gray—Higley and Raddin 1891; Pepoon 1927; Benke 1928. *A. polyphyllus* Willd. non Moench—Higley and Raddin 1891; Pepoon 1927.]

August–October. Disturbed ground in mostly unshaded habitats: roadsides, railroad rights-of-way, open woods, and pastures. Very common, weedy, recorded from every county. The range extends from s. PQ and s. ON south to GA and n. FL and at the western limit from e. SD through e. NE, e. KS, and e. OK to LA.

Several varieties of *Aster pilosus* recognized in widely circulated floristic manuals (e.g., Deam 1940; Fernald 1950; Gleason 1952; Gleason and Cronquist 1963; Steyermark 1963; and Cronquist 1980) occur in Illinois: 1) var. *pilosus*, 2) var. *platyphyllus* (Torrey & Gray) S.F. Blake [*A. ericoides* var. *platyphyllus* Torrey & Gray—Pepoon 1927], 3) var. *demotus* S.F. Blake, and 4) var. *pringlei* (A. Gray) S.F. Blake [*A. ericoides* var. *pringlei* A. Gray (1884). *A. pringlei*—Jones and Fuller 1955; G.N. Jones 1963; Mohlenbrock 1986]. The type collection for *A. pilosus* (*sensu stricto*, i.e., for var. *pilosus*) is from Illinois (Jones and Hiepko 1981); it was originally named by Michaux and is also the type for *A. villosus* (Jones and Lowry 1986). The relatively broad-leaved, densely villous to pilose plants of var. *platyphyllus* (accepted by Deam 1940; Dobbs 1963; Steyermark 1963) can be, in my opinion, produced under the influence of certain environmental conditions. For the most part, they fit quite well in typical var. *pilosus*, a view also taken by others (A. Gray 1884; Gleason 1952; Gleason and Cronquist 1963; Cronquist 1980). Recent studies suggest that vars. *pringlei* and *demotus* perhaps should be combined under the former name (Semple and Chmielewski 1985; see also Mohlenbrock 1975). My own observations tend to support this concept (including here also *A. polyphyllus*). The variety is characterized as being nearly glabrous and having relatively

narrow leaves; these plants are fairly common throughout the state. When taken in the narrow sense, however, var. *pringlei* is restricted in Illinois to Lake County (Swink 1974; Mohlenbrock and Ladd 1978; Swink and Wilhelm 1979). A great deal of intergradation between the above varieties can be found in herbarium specimens and observed in the field. I have not attempted, therefore, to elaborate on keys in the literature dealing with varieties of this variable species (see Deam 1940; Fernald 1950; Gleason 1952; Gleason and Cronquist 1963; Steyermark 1963; and Cronquist 1980).

21. *Aster praealtus* Poir.
Willow-leaved Aster,
Willow Aster



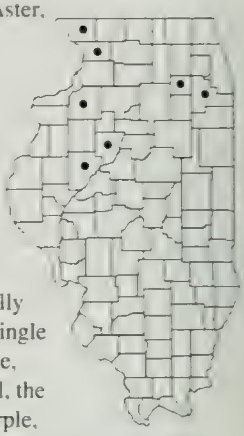
Herbaceous, with a strongly creeping rhizome system, the connecting strands often persistent for several seasons. **New shoots** mostly originating at the tips of fleshy stoloniform rhizome strands, the plants forming extensive colonies. **Stems** commonly single at any point of emergence, stout, erect, sometimes slightly reddish or glaucous, (40)60–150 cm tall, with ascending branches above the middle, variously hispidulous to hirsute, the indument in decurrent lines from the nodes or sometimes uniformly distributed around the stem, especially on the branchlets, the lower stem portion glabrescent. **Leaves** polymorphic, the basal and lower cauline ones commonly withered and deciduous at flowering time; basal rosette leaves fleshy, spatulate, 4–7 cm long and 1–2.5 cm wide, deep green above and often purplish below, with several pairs of anastomosing secondary nerves, minutely scabrous above, glabrous below, the apex rounded, the margins entire or shallowly serrate, ciliate on the narrowed subpetiolar portion, the base dilated and sheathing; principal cauline leaves firm, sessile, elliptic to linear-lanceolate, 4–12(15) cm long and 0.3–1.5 cm wide, gradually reduced in size upward on the stem, rugulose, with indistinct secondary nerves but a conspicuous reticulum of brownish tertiary veins (notable on the lower surface), enclosing isodiametric areolae, the upper surface commonly scabrous at least near the margins, sometimes strongly so, rarely glabrous, the lower surface mostly glabrous (in Illinois plants) or sometimes puberulent, the apex acute to attenuate with a sharp callus point, the margins frequently inrolled, entire or shallowly serrate, and scabrous, the base gradually tapered, often slightly rounded, decurrent; leaves of the upper stem and branches usually with clusters of smaller leaves (plus a few heads) in the axils, therefore numerous and notably unequal in size, oval to linear-lanceolate, acute or obtuse, callus-pointed, scabrous-margined; leaves of the peduncles relatively few, similar in contour, ascending or recurved-spreading, (2)4–10 mm long, flexible, not intergrading with the phyllaries but often closely subtending the head. **Capitulescence** a mostly ample, leafy, slenderly thyrsiform or broadly diffuse panicle in the terminal 1/4–1/2 stem portion, the head-bearing branchlets rarely racemiform. **Flowering heads** 1.5–2(2.5) cm in diameter when the rays are fully extended, usually not secund, on peduncles 0.3–2 cm (or more) in length. **Involucre** campanulate, (4)5–7(8) mm high, the phyllaries imbricated in 4 or 5(6) series. **Phyllaries** appressed or with slightly recurved tips, at least somewhat or often strongly graduated, the outer ones 2–3(3.5) mm, the inner (4)5–6.5 mm long; outer and median phyllaries oblanceolate, somewhat constricted above a slightly dilated base, the green areoles oblanceolate or lance-rhombic, or sometimes the outer phyllaries largely herbaceous, the abaxial surface glabrous, the adaxial surface sparsely puberulent, the apex acute to acuminate and often with a reddish callus point, the margins ciliolate, erose-hyaline, and with a narrow scarious rim extending nearly to the tip, the basal 1/2–3/4 portion scarious; innermost phyllaries very slender, linear, with linear-oblanceolate, light green areoles, the apex acuminate or attenuate. **Receptacle** alveolate with sharp teeth. **Ray florets** (15)20–30 (or more), the corollas 7–10(12) mm long, typically lavender to rose-purple (rarely white), glabrous. **Disk florets** 25–35 (or more), the corollas tubular or narrowly funnelform, 4–6.5 mm long, the limb cream-colored or light yellow turning purple after anthesis, the lobe/limb fraction 0.18–0.2, the tube much shorter than the limb. **Pappus** simple, the bristles often slightly longer

than the disk corolla, whitish, soft, slender, and attenuate. **Achenes** oblong-obovoid, plump or slightly compressed, 1.5–2 mm long and 0.5–0.8 mm across, purple, or straw-colored with purple streaks, thinly strigillose, with 4 or 5 ribs. $2n$ = 32. Including *A. subasper* Lindley in Hooker (see Wiegand 1933). [*A. salicifolius* Aiton and sensu auct. non Lam.—Brendel 1887; Higley and Raddin 1891; Pepoon 1927; G.N. Jones 1945, 1950; Fell 1955. *A. carneus* misapplied, not of Nees—Mead 1846, and many herbarium sheets so labelled.]

September–October. Low moist or swampy ground: woods, thickets, meadows, banks of streams and rivers, ditch margins, and lakeshores. Common throughout the state. The range of the species extends in the eastern half from ON, MI, and PA to n. FL and in the western half from s. MB through ND, SD, NE, and OK to TX and n. Mexico.

The plants are variable, but attempts to distinguish the varieties that have been described (Wiegand 1933) are not very successful. The reason is a high degree of morphological intergradation and an apparent lack of convincing geographic range separation. The majority of Illinois collections can be identified with typical var. *praealtus* [including var. *angustior* Wieg., pro parte (and in the sense of some authors and collectors)—Deam 1940; Steyermark 1963]. The var. *subasper* (Lindley in Hooker) Wieg., originally described (as *Aster subasper*) from the St. Louis area, has been recognized by several authors (Deam 1940; Steyermark 1963; Swink 1974; Swink and Wilhelm 1979). Plants of this variety are fairly common; they are more readily identifiable by their copiously scabrous leaves and stems than by the characters used to define the taxon in the keys of Deam (1940) and Steyermark (1963), namely cauline leaves that are relatively short and elliptic, and rameal leaves that are mostly oval and obtuse. Good evidence exists of occasional hybridization and intergradation with *A. lanceolatus* [e.g., *V. H. Chase 137* (F) from Stark Co., *Evers 109660* (ILLS) from Johnson Co., *A.G. Jones 4616* (ILL) from De Witt Co.] and with *A. puniceus* var. *firmus* (Nees) Torrey & Gray [e.g., *Winterringer 16261* (ISM) from Cook Co., *Wolf 170* (F) from Fulton Co., *Wade & Wade 2383* (F) from Ogle Co., and others].

22. *Aster prenanthoides* Muhl. ex Willd.
Crooked-stemmed Aster,
Crooked Aster

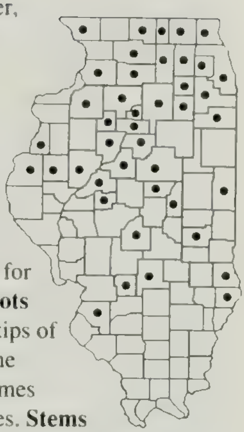


Herbaceous, with a creeping rhizome system. **New shoots** produced at the tips of stoloniform rhizome strands, the plants typically colonial. **Stems** mostly single at any point of emergence, erect, (40)60–120 cm tall, the older ones often dark purple, branched near or commonly above the middle, the branches zigzag, somewhat angled in cross section from decurrent leaf bases, villous or hirsute in decurrent lines, the indument sometimes uniformly distributed on the peduncles, the lower portion of the stem glabrescent or glabrous. **Leaves** polymorphic, those of the basal rosettes subpetiolate, the blades obovate to oblanceolate, 1.5–7 cm long and 1–2 cm wide, with several pairs of anastomosing secondary nerves, scabrellous above or glabrous on both surfaces, acute or obtuse, crenate to crenate-serrate, abruptly narrowed to a slender or slightly winged petiolelike portion, with long marginal cilia and an often reddish, dilated, sheathing base; principal cauline leaves mostly persistent throughout the flowering period, subsessile or sessile, oblanceolate in outline but abruptly and strongly contracted near or below the middle, 8–16(20) cm long and 1.5–5.5 cm wide, gradually reduced in size upward on the stem, the blades with 6–10 (or more) pairs of anastomosing secondary nerves; nerves in the wider, apical portion pinnate, those in the narrower, basal portion running parallel to the midrib, the reticulum of tertiary veins weakly expressed with irregular areolae, the upper surface scabrellous, the lower minutely strigillose or glabrous but commonly hispidulous or villous along the midrib, the apex long-acuminate with a callus point, the margins sharply serrate, with callus-pointed teeth on the wider blade portion but commonly entire on the narrowed portion, the base dilated and strongly auriculate-clasping, the midrib extended on the stem as a decurrent ridge;

rameal leaves similar in most aspects but often only slightly contracted near the middle, glabrous or nearly so, the margins less sharply toothed or often entire, the base sessile and clasping; leaves of the peduncles relatively few, lanceolate, 3–12 mm long, not intergrading with the phyllaries. **Capitulescence** a broad, flat- or round-topped, dichotomously branched panicle in the upper $^{1}/_{4}$–$^{1}/_{2}$ portion of the stem, the branches slender, sometimes purplish. **Flowering heads** (1.8)2–2.5 cm in diameter when the rays are fully extended, not crowded and not secund, on slender peduncles 1–4 cm in length. **Involucre** campanulate or hemispheric, 5–6 mm high, the phyllaries imbricated in 4 or 5(6) series. **Phyllaries** often only slightly graduated, flexible, with recurved or sometimes reflexed tips, the outer ones mostly lanceolate and slightly constricted near the middle, 2.5–4 mm long, the inner and median ones linear-oblanceolate, 4–5 mm long, the green areoles linear-oblanceolate, or sometimes the outer phyllaries largely herbaceous, the abaxial surface glabrous, the adaxial surface slightly puberulent, the apex acute and callus-pointed, the margins irregularly ciliolate, erose-hyaline, and with a narrow scarious rim extending nearly to the tip, the basal $^{1}/_{3}$–$^{1}/_{2}$ portion scarious. **Receptacle** alveolate with blunt teeth. **Ray florets** 18–25 (or more), the corollas 10–15 mm long, typically lavender or bluish (rarely white), glabrous. **Disk florets** 20–25 (or more), the corollas funnelform, (3.5)4–5 mm long, often thinly puberulent near the throat, the limb cream-colored or light yellow turning purple after anthesis at least in the lobes, the lobe/limb fraction 0.2–0.25, the tube slightly shorter than the limb. **Pappus** simple, the bristles as long as or slightly shorter than the disk corolla, somewhat discolored, soft, slender, and attenuate. **Achenes** cylindric-oblanceolate or obovoid, slightly compressed, 2–3(3.5) mm long and 0.5–0.8 mm across, dull purple or straw-colored, thinly strigillose, 4- or 5-ribbed. $2n = 32$ (mostly), 48.

Late August–October. Moist or swampy ground: woods, thickets, meadows, seeps, and stream banks. Occasional, recorded by me from only seven counties in Illinois, much more common to the east. The range of the species extends from s. ON, NY, and PA south to NC and TN and west to MN and IA.

23. *Aster puniceus* L.
Purple-stemmed Aster,
Red-stemmed Aster,
Swamp Aster



Herbaceous, with a horizontal, short or often strongly creeping rhizome system, the connecting strands persistent for several seasons. **New shoots** mostly originating at the tips of fleshy stoloniform rhizome strands, the plants sometimes forming extensive colonies. **Stems** mostly single at any point of emergence, stout, erect, commonly purplish or maroon-colored, 50–150(180) cm tall, with ascending or divaricate branches in the upper half, variously hirsute to hispidulous (or both) in decurrent lines from the nodes, or the indument nearly uniformly distributed around the stem, the basal portion sometimes coarsely hispid. **Leaves** polymorphic, the basal and lower cauline ones commonly withered and deciduous at flowering time, but the head-bearing branchlets often very leafy (var. *firmus*); basal rosette leaves spatulate or oblanceolate, 3–10 cm (or more) long and 0.3–2 cm (or more) wide, dark green and somewhat rugulose above, often purplish below, the venation and vestiture similar to that of the principal leaves, the apex acute to rounded, the margins remotely crenate-serrate to subentire, the lower subpetiolar portion of the blade winged, dilated, and sheathing at the base; principal cauline leaves variable, firm, sessile, (6)10–15(20) cm long and (1)2–5 cm wide, gradually reduced in size upward on the stem, with several pairs of pinnate and anastomosing secondary nerves, and a reticulum of tertiary veins with isodiametric or oblong areolae, the upper surface scabrous or glabrous, often glossy (resulting from the presence of bulliform epidermal cells), the lower surface glabrous or minutely strigillose and often with scabrous, hispidulous, or villous indument along the midrib, the apex acute, acuminate, or attenuate, with a callus point, the margins shallowly serrate to subentire, the base typically clasping, often strongly auricled in the lower leaves, sometimes merely rounded and decurrent in those higher up

on the stem; rameal leaves often numerous, elliptic-lanceolate to linear-lanceolate, gradually reduced, acute to attenuate, callus-pointed, the vestiture similar to that of the larger leaves, the margins subentire to entire and often inrolled, the midrib and larger nerves commonly extending downward on the stem as decurrent or almost winged ridges; leaves of the peduncles relatively few, 0.5–2 cm long, flexible, somewhat constricted above a dilated base, often closely subtending the head and appearing to be a part of the involucre, but rarely bracteiform. **Capitulescence** an often ample, leafy, broad, round- or flat-topped, more or less dichotomously branched panicle in the upper $^1/_4$–$^1/_2$ stem portion, the branches ascending or divaricate. **Flowering heads** 1.5–3.5(4) cm in diameter when the rays are fully extended, typically not secund, subsessile and overtopped by the subtending rameal leaves, or often on densely hirsute to villous peduncles 0.2–3 cm (or more) in length. **Involucre** campanulate, (6)8–12(15) mm high, the phyllaries imbricated in 4–6 series. **Phyllaries** typically not or only somewhat graduated, 6–10(15) mm long, flexible, leaflike, the outer ones often appreciably longer than the inner and largely herbaceous; phyllaries of the 2nd and 3rd series inward lanceolate to linear-oblanceolate, often spreading or reflexed, somewhat constricted above a slightly dilated base, glabrous (rarely slightly scabrous) on the abaxial surface and thinly puberulent on the adaxial surface, the apex attenuate or acute to obtuse (depending on the variety), and callus-pointed, the margins irregularly ciliolate or lanate, the scarious basal portion typically much smaller than the green portion and often indurate or slightly keeled; innermost phyllaries very slender, linear, with linear-oblanceolate, light green areoles in the apical $^1/_2$–$^2/_3$ portion, the margins erose-hyaline and with a scarious rim. **Receptacle** alveolate with sharp teeth. **Ray florets** 20–40 (or more), the corollas 12–18(20) mm long, lavender to deep bluish purple (rarely white), glabrous or slightly puberulent on the throat and tube. **Disk florets** (20)30–50 (or more), the corollas narrowly funnelform, abruptly dilated at the throat, (4.5)5–6 mm long, glabrous or with a few trichomes, the limb cream-colored or yellow turning pink or purple after anthesis, the lobe/limb fraction 0.2–0.3, the tube shorter than the limb. **Pappus** simple, the bristles about as long as the disk corolla, whitish or slightly discolored, soft, slender, and attenuate. **Achenes** oblong or oblanceolate in contour, often somewhat falcate, plump or slightly compressed, (2)2.5–3.5(4) mm long and 1 mm or less across, purple at maturity or brown when weathered, thinly puberulent or glabrescent, 4- or 5-ribbed. $2n = 16$ (typically), 32. Including *A. firmus* Nees and *A. lucidulus* (A. Gray) Wieg. (see A.G. Jones 1984, 1987). [*A. novi-belgii* misapplied, not of L.—Brendel 1887; Higley and Raddin 1891; Mohlenbrock 1975, 1986. *A. longifolius* misapplied, not of Lam.—Pepoon 1927; Fell 1955; Jones and Fuller 1955. *A. patens* misapplied, not of Aiton—Higley and Raddin 1891; Pepoon 1927.]

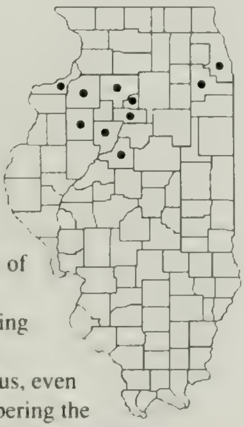
(Late August) September–October. Low moist or swampy ground: woods, thickets, meadows, banks of streams and rivers, ditch margins, and lakeshores. Common in the northern two-thirds of the state, extending south to St. Clair, Bond, Fayette, and Lawrence counties. The range of the species (*sensu lato*) extends in the East from NF and LB south to FL, and in the West from SK and AB to ND, with a few scattered records from SD, e. NE, IA, MO, and from Van Zandt and Smith counties in n.e. TX.

The plants are extremely variable, but two morphologically well-delimited varieties can be distinguished in Illinois: var. *puniceus* [including f. *demissus* (Lindley) Fern.—Dobbs 1963] and var. *firmus* (Nees) Torrey & Gray [*Aster firmus*—Mohlenbrock 1986. *A. puniceus* var. *lucidulus* A. Gray—Higley and Raddin 1891; Pepoon 1927; Mohlenbrock 1975. *A. lucidulus*—Deam 1940; G.N. Jones 1945, 1950, 1963; Gleason 1952; Jones and Fuller 1955; Gleason and Cronquist 1963; and others. *A. puniceus* subsp. *firmus* (Nees) A.G. Jones (1984)]:

1. Stems nearly glabrous or glabrescent in the lower half, hirsute or sparsely hispidulous in lines in the upper portion; lower leaf surface glabrous or sparsely scabrous along the midrib; phyllary tips short-attenuate or often acute to obtuse; rhizomes with strongly creeping stoloniform strands .... var. *firmus*
1. Stems hispidulous over the entire length, the indument at least in part uniformly distributed around the stem; lower leaf surface minutely strigillose, the midrib hispidulous or densely hirsute to villous; phyllary tips generally long-attenuate; rhizomes with short, thick, fleshy strands .... var. *puniceus*

The ranges of these two varieties in Illinois are overlapping, but plants of var. *firmus* seem to be more common than those of var. *puniceus*. Attempts to separate the two taxa at the level of species have been frustrated because of a high degree of intergradation and inconstancy in the character states. There is also evidence of intergradation between *Aster puniceus* and such other members of the $x = 8$ chromosome number assemblage as *A. lanceolatus* [e.g., *Bebb s.n.* (F 17355) from Winnebago Co. and *Wade & Wade 1744* (ISM) from Ogle Co.], *A. lateriflorus* (see Steyermark 1963), and *A. praealtus* [e.g., *Smith 667* and *683* (F) from Cook or Du Page Co. and *Shildneck 11617* (ILL) from Fayette Co.]. Illinois specimens that have been labelled *A. longifolius* belong mostly in *A. puniceus* var. *firmus*. Although G.N. Jones (1950, 1963) in his keys treated *A. longifolius* in accordance with Lamarck's type and circumscription, the species probably does not get into Illinois. The collections cited by Pepoon (1927) for *A. patens* [*Raddin* (F) and *Umbach* (F)] belong in *A. puniceus* var. *firmus*, not in *A. laevis* as suggested by Swink and Wilhelm (1979).

24. *Aster schreberi* Nees
Schreber's Aster



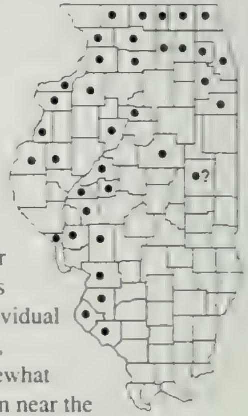
Herbaceous, with a strongly creeping horizontal rhizome system. **New shoots** arising mostly at the ends of stoloniform rhizome branches, the plants forming extensive colonies; basal rosettes typically numerous, even in midseason far outnumbering the flowering stems and often forming a dense ground cover. **Flowering stems** single at any point of emergence, erect, 30–80 cm tall, terete or, at the upper nodes, somewhat angular in cross section from decurrent nerves, the ascending or divaricate branches mostly confined to the capitulescence, the main stem sometimes reddish, glabrous, the branches sparsely scabrous or puberulent, sometimes in decurrent lines, but the indument usually uniformly distributed on the peduncles. **Leaves** polymorphic, those of the basal rosettes and the lower half of the stem petiolate; basal rosette leaves largest, the blades broadly ovate to cordate, (8)10–25 cm long and (6)8–16 cm wide, with 5–8 pairs of pinnate secondary nerves, and a weakly expressed reticulum of tertiary veins with mostly isodiametric (rarely oblong) areolae, the upper surface glabrous or thinly scabrous, the lower with a few trichomes along the nerves, the apex acuminate with a sharp mucro, the margins coarsely and often irregularly crenate-serrate, each tooth with a clear or green to purplish mucro, the base deeply cordate, the lobes sometimes overlapping or the sinuses often broad, the petioles 1–2 times as long as the blades, with slightly winged and glabrous or sparsely ciliate margins, somewhat dilated and sheathing at the base; cauline leaves gradually reduced in size upward on the stem, blades of the larger ones often nearly as wide as long, similar to the basal leaves in contour and indument except for the progressively shorter and gradually more broadly winged petioles; upper cauline leaves subpetiolate or sessile, elliptic or obovate, with a truncate or cuneate base; rameal leaves relatively few, abruptly reduced, variable in size, ovate or oval, subglabrous or the indument similar to that of the larger leaves, the apex acute or acuminate, the margins finely and sharply serrate and ciliate, the base rounded or cuneate; leaves of the peduncles 0–few, ovate-lanceolate, 2–3 mm long, flexible, attenuate, entire, ciliate, not intergrading with the phyllaries. **Capitulescence** a terminal corymbiform panicle, but often also with lateral flowering branches from the upper nodes of the main stem, the cymule-bearing branchlets stiffly divaricate or dichotomous, the peduncles (if developed) usually ascending at a wide angle, 0.3–2 cm long, slender, typically not glandular (rarely with a few stipitate glands). **Flowering heads** variable, 2–2.5 cm in diameter when the rays are fully extended, sometimes crowded and sessile in the individual cymules. **Involucre** campanulate (turbinate when pressed), 5–7 mm high, the phyllaries imbricated in 4 or 5 series. **Phyllaries** strongly graduated, appressed when fresh (loosely spreading in fruiting heads and when pressed and dried), those of the outer 2 series oblong-ovate, 1–2(2.5) mm long, glabrous or slightly puberulent on the back, not glandular (rarely with a few minute glands at the tips), the green areoles oblong to oblanceolate (rarely

extending to the base as a broad band), the margins usually densely lanate and with a scarious rim, the basal ($^1/_3$)$^1/_2$–$^2/_3$ portion of the phyllaries scarious, indurate, and keeled or rounded on the back; phyllaries of the inner 2 series linear-lanceolate, 4.5–6(7) mm long, glabrous, largely scarious or only the midrib green, the apex often reddish. **Receptacle** alveolate with sharp teeth. **Ray florets** 6–8(12), the corollas (8)10–12(15) mm long, white or cream-colored, glabrous. **Disk florets** 15–25 (or more), the corollas funnelform, (5)5.5–7 mm long, glabrous, or thinly puberulent on the slender, tubular portion of the limb, the limb strongly flared ca 1.5 mm above the point of insertion of the filaments, cream-colored or light yellow aging to purple, the lobes reflexed, the fraction of lobe/expanded limb portion 0.4–0.5, the apparent tube (i.e., including the tubular limb portion) distinctly longer than the expanded limb portion. **Pappus** tawny, the bristles in 2 series, those of the inner series about as long as the disk corolla, firm, with a clavellately expanded apex, those of the outer somewhat shorter, more slender, and attenuate. **Achenes** slenderly fusiform, 3–5 mm long and 1–1.2 mm across, dull purple or light chocolate brown, glabrous or with a few scattered trichomes near the top, with (7)8–10 thick (sometimes double-stranded) straw-colored ribs. $2n = 54$. Including *A. chasei* G.N. Jones in Jones & Fuller (1955).

Late July–September. Mesic but usually well-drained loamy or gravelly soil in wooded areas: plants in Illinois found mostly on north-facing slopes of ravines or along streams and rivers ca 30–60 m (or more) above the water level. Occasional in the northern one-third of the state, south to Tazewell County and west to Rock Island, Henry, and Knox counties. Illinois (and Wisconsin) records represent the western outpost of this species, disjunct by ca 450 km from the nearest populations to the east. The species range extends from ME west through s.e. ON to s.e. WI and south through PA, WV, and s.e. OH to VA, e. KY, e. TN, and n. AL.

Aster schreberi has been included in the Illinois list of threatened species, but the plants are of rather common occurrence in the piedmont and mountain woods of the eastern and southeastern states. I have so far been unsuccessful in a search for consistent characters whereby the midwestern populations [sometimes treated as *Aster chasei*—G.N. Jones 1963] can be distinguished from those to the east, at least at the varietal level. The plants also share the same hexaploid chromosome number of $2n$ (= $6x$) = 54.

25. ***Aster sericeus*** Vent.
Silky Aster



Herbaceous, with a cormoid-caudiciform rhizome system that turns woody with age. **New shoots** initiated at or near the base of old stems resulting in scattered individual clumps. **Stems** 1–several, slender, erect, wiry, somewhat fastigiately branched from near the middle, 20–70 cm tall, aging to light brown, glabrous in the lower half, thinly soft-pubescent in the middle portion, and sericeous-strigose in the branchlets. **Leaves** relatively uniform, sessile, entire, appressed sericeous to densely silvery-silky on both surfaces including the margins, the basal and lower cauline ones often withered and deciduous at flowering time; basal rosette leaves oblanceolate or spatulate, with 1 or 2 pairs of secondary nerves arching forward from the base in alignment with the margins, the surfaces less copiously pubescent than those of the cauline leaves, the apex acute, the base sheathing; principal cauline leaves slightly or gradually reduced upward on the stem, oblong to linear-lanceolate, 1.5–3(5) cm long and 4–10 mm wide, the apex mucronulate, the base rounded but not clasping; rameal leaves similar in contour and vestiture, flexible, acute, spinulose-mucronulate, those of the peduncles crowded, 4–8(10) mm long, intergrading with the phyllaries. **Capitulescence** an open, somewhat fastigiately branched panicle in the upper $^1/_2$–$^2/_3$ portion of the stem, the branchlets often arching. **Flowering heads** 2–3 cm in diameter when the rays are fully extended, usually not crowded and not secund, subsessile or on peduncles 0.5–3(5) cm in length. **Involucre** cylindric to narrowly campanulate, 5–8(10) mm high, the phyllaries imbricated in 3–5(6) series. **Phyllaries** graduated or sometimes subequal, spreading or squarrose to reflexed, sericeous on both surfaces, including the scarious basal portion and the margins; outer phyllaries

(4)5–6 mm long, often largely herbaceous, ovate, acute, mucronulate, the median ones 6–8(10) mm long, ovate-lanceolate, acuminate or attenuate, green in the expanded apical 1/2–2/3 portion, the abruptly narrowed basal portion scarious, indurate, and rounded on the back; innermost phyllaries very slender, attenuate, often reddish at the base. **Receptacle** strongly alveolate with sharp teeth. **Ray florets** (10)15–25, the corollas 12–15(18) mm long, deep purple (rarely white), with a few trichomes near the throat. **Disk florets** 20–30 (or more), the corollas narrowly funnelform, (5)6–7 mm long, thinly puberulent on the tube and throat, the limb bright yellow turning reddish purple after anthesis, the lobe/limb fraction 0.18–0.2, the tube much shorter than the limb. **Pappus** simple, the bristles about as long as the disk corolla, discolored or tawny, relatively firm, attenuate. **Achenes** fusiform, plumpish, 2–3 mm long and 0.7–1 mm across, purple at maturity or brown when weathered, glabrous, prominently 7–10 ribbed. $2n = 10$.

Late August–October. Dry sandy, loamy, or rocky soils in unshaded situations: sand barrens, dunes, hill prairies, and open-wooded bluffs. Local, mostly in the northern half of the state, but extending southward along the Mississippi River to Randolph County. The range of the species extends from s. ON and MI to TN, and in the West through the eastern half of the Great Plains from s.e. MB to TX.

Illinois plants belong in var. *sericeus*.

26. ***Aster shortii*** Lindley in Hooker
Short's Aster

Herbaceous, with branched-caudiciform or short horizontal rhizomes that turn woody with age. **New shoots** initiated at or near the base of old stems resulting in scattered individual clumps. **Stems** 1–several, erect, (40)80–120 cm tall, much branched and bushy, densely and uniformly soft-hirtellous on the upper stem and in the branches, the indument in decurrent lines farther down, or the stem glabrescent in the lower portion. **Leaves** polymorphic, the basal and principal cauline ones petiolate; leaves of new shoots and of the vernal rosettes with the blades mostly ovate, 1–6 cm long and 1–3.5 cm wide, dark green above, purplish below at least during the cool season, with 1 or 2 pairs of anastomosing secondary nerves curving forward from the base and additional pinnate nerves emanating from the midrib, the apex acute or obtuse, the margins crenate, the base cordate or rarely truncate; petioles twice as long as the blades, slender, not at all or only narrowly winged, often densely pilose or hirsute; principal cauline leaves largely persistent throughout the flowering period, regularly spaced, the internodes 2–3(4) cm long, the blades ovate to lanceolate, sometimes falcate, 5–10(15) cm long and 2–7 cm wide, often conspicuously rugulose, with several pairs of pinnate and anastomosing secondary nerves, and a reticulum of tertiary veins with more or less isodiametric areolae, the upper surface glabrous, or slightly scabrous along the midrib, the lower surface copiously hirtellous or hirsute, the apex acute to attenuate or acuminate and with a sharp callus point, the margins mostly entire and scabrous, or shallowly crenate-serrate in the lower leaves, the base cordate, truncate, or rounded, sometimes oblique, the petioles half as long as the blades or less, slender, not sheathing or clasping; rameal leaves more or less abruptly reduced in size, lanceolate to ovate, entire, sessile, or sometimes with short petioles, densely hirtellous, acute or obtuse with a sharp, often purple callus point; leaves of the peduncles minute, bracteiform, 1–1.5 mm long, intergrading with the phyllaries. **Capitulescence** an ample, diffuse, broad-topped panicle, the head-bearing branchlets often arching. **Flowering heads** 1.5–2.5 cm in diameter when the rays are fully extended, usually not crowded and not secund, the peduncles densely bracteate, 0.2–3(5) cm long, hirtellous. **Involucre** campanulate (or hemispherical when pressed and dried), 4.5–6 mm high, the phyllaries imbricated in 5 or 6 series. **Phyllaries** appressed when fresh, strongly graduated, the outer triangular or lanceolate, 1–1.5 mm long, the inner linear-lanceolate, 4–5.5 mm long, puberulent on both surfaces, the green areoles oblanceolate to rhombic in the apical 1/6–1/4(1/2) portion, usually much shorter than the scarious basal portion (rarely the outer phyllaries with a green band to the base), the apex acute or

acuminate, the margins erose-hyaline and irregularly ciliolate. **Receptacle** alveolate with sharp teeth. **Ray florets** (15)18–25, the corollas 10–15 mm long, typically deep blue or purple, glabrous. **Disk florets** 20–25 (or more), the corollas funnelform, 5–6 mm long, glabrous or nearly so, the limb abruptly dilated at the throat, light yellow turning reddish purple after anthesis, the lobe/limb fraction 0.18–0.2, the tube shorter than the limb. **Pappus** simple, the bristles about as long as the disk corolla, tawny or rose-tinged, soft, slender, and attenuate. **Achenes** oblong-obovoid, somewhat compressed, 2.5–3 mm long and ca 1 mm across, dull purple at maturity or brown when weathered, glabrous, with 4 or 5 ribs. $2n = 16$; reported chromosome counts of $2n = 18$ are probably in error (A.G. Jones 1977).

September–October. Well-drained soils: edges of upland woods, thickets, wooded river banks, and open-wooded slopes. Common nearly throughout the state.The species range extends from s. ON, w. PA, and n.w. MD, south to GA, n. FL, and AL, west to e. MN and e. IA with scattered records from AR (but apparently none from MO).

Plants in Illinois belong in var. *shortii*, including f. *gronemanii* Benke, described as a plant with rose-red rays from a collection made near Elgin, Kane County [*Benke 4872* (F)]. There is evidence of occasional hybridization and intergradation with *Aster anomalus* and *A. urophyllus* [e.g., *Fell 53-1005* (ILL) from De Kalb Co. and *Winterringer 14794* (ISM) from Jersey Co.], and with other related species.

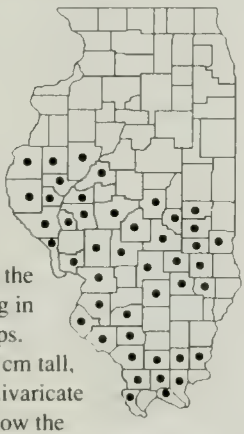
27. **Aster tataricus** L.f.
Tartarian Aster

Herbaceous, with a branched cormoid-caudiciform rhizome system but also producing short, fleshy, stoloniform rhizome strands. **New shoots** arising from nodes and tips of rhizomes and also from many winter buds just below the base of old stems, the plants aggressively spreading by vegetative reproduction. **Stems** 1–several, stout, erect, 80–150 cm tall, somewhat angled and ridged from decurrent leaf bases, branched only in the capitulescence, uniformly hirtellous or scabrous with antrorsely hooked trichomes. **Leaves** polymorphic, the basal ones most prominent forming convoluted clusters rather than rosettes, very coarse, 3–4 times as large as the largest cauline leaves, the blades oblanceolate, 10–30 cm long and 5–10 cm wide, strongly rugose, with 6–12 pairs of pinnate and anastomosing secondary nerves, the upper surface minutely scabrous, the lower surface densely scabrous or puberulent especially along the nerves, the apex acute, obtuse, or rounded, and mucronate, the margins crisp, crenate-serrate, each tooth with a conspicuous mucro, the base of blades gradually tapered, the petioles winged, 10–40 cm long, as long as the blades or longer, sheathing at the base; cauline leaves gradually reduced upward on the stem, (8)10–15(18) cm long and 2–5 cm wide, relatively densely spaced with internodes 2–4 cm long, the lower leaves oblanceolate and subpetiolate, the upper lanceolate and sessile, similar to the basal leaves in surface, venation, and indument, the apex acute or acuminate and mucronulate, the margins serrate or entire, densely ciliolate, the base cuneate, sheathing, and decurrent; rameal leaves abruptly much reduced in size, lanceolate, 0.5–1 cm long, puberulent, acute or attenuate and mucronulate, those of the peduncles few, bracteiform but flexible, not phyllarylike. **Capitulescence** an elongate or broad-topped panicle in the upper $^1/_6$–$^1/_3$ of the stem, the terminal branchlets short with few-headed corymbiform clusters. **Flowering heads** 2–2.5(3) cm in diameter when the rays are fully extended, sessile in the axils of subtending leaves or on puberulent and somewhat ridged peduncles 0.5–1.5(2.5) cm long. **Involucre** campanulate or hemispherical, 6.5–8(10) mm high, the phyllaries imbricated in 5 or 6 series. **Phyllaries** appressed or somewhat spreading, graduated, those of the outer series triangular or lanceolate, 3–4 mm long, those of the inner series linear-lanceolate, 6–8 mm long, glabrous or minutely puberulent, with green bands along the midrib to the base, or the outer phyllaries sometimes largely herbaceous, the apex acute in those of the outer 2 series, attenuate in those farther inward, the margins entire or erose-hyaline and with a red rim. **Receptacle** alveolate with sharp teeth. **Ray florets** 15–18(20), the corollas 10–15(18) mm long, lavender, glabrous. **Disk florets** 20–30 (or more), the corollas funnelform, (4.5)5–6 mm long, glabrous or with a few trichomes at the throat, the limb abruptly dilated, light yellow turning lavender after anthesis at least in the

lobes, the lobe/limb fraction 0.2, the lobes notably recurved, the slender tube slightly shorter than the limb. **Style branches** somewhat atypical for the genus in having acutish rather than attenuate sterile appendages. **Pappus** simple, the bristles shorter than the disk corolla, white or cream-colored, soft, slender, and attenuate. **Achenes** obconic-obovoid, slightly compressed or plump, 1.5–2 mm long and ca 1 mm across, light brown, thinly strigillose, with 4 or 5(6) ribs. $2n = 54$.

October. Disturbed ground: roadsides, thickets, and waste places. Occasionally escaped from cultivation. Introduced from n.e. Asia. Recorded by me from Champaign, Montgomery, Sangamon, St. Clair, and Vermilion counties.

28. *Aster turbinellus* Lindley in Hooker



Herbaceous, with stout, branched, caudiciform rhizomes that turn woody with age. **New shoots** initiated at or near the base of old stems resulting in scattered individual clumps. **Stems** 1–several, 50–100 cm tall, with many ascending or divaricate branches from near or below the middle, glabrous or hirtellous in thin decurrent lines. **Leaves** polymorphic, notably variable in size, the lower ones soon withered and deciduous; basal rosette and lower cauline leaves subpetiolate, the blades oblong-oblanceolate, glabrous, the apex acute, obtuse, or rounded, the margins shallowly crenate and ciliolate, the subpetiolar portion coarsely ciliate, winged, and slightly dilated toward a sheathing base; principal leaves gradually reduced upward on the stem, sessile, firm, linear-oblanceolate to elliptic-lanceolate, gradually tapered at both ends, 4–12 cm long and 0.5–2 cm wide, with a prominent midrib and weakly expressed anastomosing secondary nerves, the upper surface glabrous, the lower surface scabrous only along the midrib, the apex acute with a sharp callus point, the margins mostly entire, ciliolate, the base cuneate or rounded and hugging the axillary branchlets; rameal leaves similar in contour, those of the peduncles often densely spaced, bracteiform, appressed or ascending, oblong to subulate, 1.5–4 mm long, continuous with the phyllaries but distinct in having a pointed apex with a brown or purple mucro. **Capitulescence** an open, broad, round-topped panicle. **Flowering heads** 2–3 cm in diameter when the rays are fully extended, not crowded and not secund, usually at the ends of wiry, ascending or divaricate, few- to many-bracted peduncles (1)4–10(25) cm in length (rarely sessile). **Involucre** slenderly campanulate or turbinate, 7–12 mm high, the phyllaries imbricated in 6–9 series, inserted on a prominent obconical rachis 2–4 mm in height. **Phyllaries** strongly graduated, appressed or somewhat spreading, indurate, rounded on the back or slightly keeled, the green areoles well delimited, oblong to rhombic-oblanceolate, centered in the apical $^{1}/_{5}$–$^{1}/_{3}$ portion, usually much shorter than the scarious basal portion, the apex obtuse, rounded, or almost truncate, sparsely lanate, including the top (areolar) portion of the adaxial surface, the margins with a comparatively broad scarious rim extending to the tip; outer (lowermost) phyllaries ovate, 1.5 mm long, the median and inner ones linear, to 7 mm long. **Receptacle** alveolate with sharp teeth. **Ray florets** 15–20, the corollas 10–15 mm long, blue or purple, glabrous. **Disk florets** 15–20 (or more), the corollas narrowly funnelform, 4.5–6(7) mm long, glabrous, the limb yellow turning purple after anthesis at least in the lobes, the lobe/limb fraction 0.18, the tube sightly shorter than the limb. **Pappus** simple, the bristles about as long as the disk corolla, tawny or somewhat rose-tinged, comparatively firm, attenuate. **Achenes** oblong in contour, somewhat compressed, (1.8)2–2.8 mm long and ca 1 mm across, light brown or gray, puberulent or minutely strigillose, often puncticulate, with 3–5 ribs. $2n = 96$, sometimes with additional B-chromosomes.

Late August–October. Dry loamy or rocky soils: edges of upland woods, open-wooded slopes and bluffs, and also in somewhat disturbed ground of pastures and roadsides. Local, mostly in the southern half of the state, north to Macon, Fulton, and McDonough counties. Records from Illinois represent the northern and northeastern limits for the species. The range extends southward to n. LA and westward through s. MO and AR to e. NE, s.e. KS, and e. OK.

29. *Aster umbellatus* Miller
Flat-top Aster

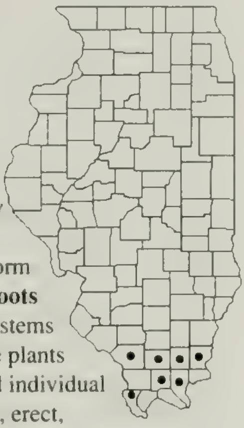
Herbaceous, with a creeping horizontal rhizome system. **New shoots** initiated at intervals along or at the ends of stoloniform rhizome strands resulting in colonial stands; autumnal rosettes lacking. **Stems** mostly single at any point of emergence, erect, 50–150 cm tall, usually unbranched below the capitulescence, glabrous in the lower portion, commonly puberulent with antrorsely hooked trichomes above, the branches somewhat winged or ridged from decurrent leaf bases. **Leaves** (except the lowermost) more or less uniform in contour, sessile or subpetiolate, those of the midstem ovate to elliptic-lanceolate, 4–12 cm long and 1–3(4) cm wide, with a prominent midrib that is abaxially keeled in the basal or subpetiolar portion and with 6–8 pairs of pinnate and anastomosing secondary nerves, as well as a conspicuous reticulum of tertiary veins with isodiametric areolae, the upper surface dark green, glabrous or minutely scabrous, the lower surface bluish green, scabrous-puberulent, at least along the midrib and major nerves, the apex acuminate, the margins entire, scabrous, the base cuneate and decurrent; lower cauline leaves smaller, often spatulate, those near ground level bracteiform; rameal leaves relatively few, much reduced in size but otherwise resembling the larger leaves except for the few small, subulate, puberulent bracts subtending the head. **Capitulescence** flat- or round-topped, each individual cluster corymbiform. **Flowering heads** 1–1.5(2) cm in diameter when the rays are fully extended, often crowded, subsessile, or on slender puberulent peduncles 0.2–2.5 cm in length. **Involucre** campanulate or turbinate, 3.5–4.5(5) mm high, the phyllaries imbricated in 4 or 5 series. **Phyllaries** strongly graduated, the outer ones 1–2 mm long, the inner 3–4(6) times as long, more or less appressed at flowering time but widely spreading in fruiting heads, puberulent or glabrous on the back; outer (lowermost) phyllaries subulate, the median and inner ones oblong to linear-lanceolate, the green areoles forming broad bands to the base as an extension of the midrib, the apex acute to obtuse or sometimes rounded, the margins erose-hyaline and irregularly ciliolate. **Receptacle** alveolate with long sharp teeth. **Ray florets** (2)6–15 (or more), the corollas 8–10 mm long, often with a few trichomes on the slender tube, the rays whitish, comparatively broad, 2–3 mm wide. **Disk florets** (8)12–20, the corollas funnelform, 4–7 mm long, thinly puberulent on the tube, the limb partway slenderly tubular, abruptly flared ca 1 mm above the point of insertion of the filaments, cream-colored turning purple after anthesis, the lobes relatively long and reflexed, the fraction of lobe/expanded limb portion 0.6–0.7, the apparent tube (i.e., including the tubular limb portion) distinctly longer than the expanded limb portion. **Pappus** "double" (according to literature references) but actually composed of 3 series of bristles, whitish or somewhat discolored; bristles of the inner series about as long as the disk corolla, firm, clavellately expanded toward an acute apex, those of the middle series slightly shorter, tapered toward an attenuate apex, and those of the outer series minute, 1 mm long or less, slender, and attenuate. **Achenes** obovate to oblanceolate in contour, compressed, 2.5–3.5 mm long and 1–1.2 mm across, light brown, sparsely puberulent (Illinois plants) or sometimes glabrous, with 5 or 6 prominent, glossy, golden-brown ribs. $2n = 18$. Including *A. pubentior* Cronquist (1947). [*Doellingeria umbellata* (Miller) Nees; *A. infirmus* misapplied, not of Michaux—Brendel 1887.]

(Late July) August–September (early October). Low, damp, mostly open ground: swamps, seep areas, thickets near streams and rivers, and clearings in woods. Occasional in the northern half of the state, south to Menard and Cass counties. The range of the species extends from NF south to GA, n. FL, LA, s. AR, and e. TX, west to e. AB, SK, and ND, with a few stations in IA, NE, and s. OK.

Based solely on geographic considerations, plants of Illinois would be placed in var. *pubens* A. Gray (cf. Fernald 1950) or, at the rank of species, in *Aster pubentior* (cf. Gleason 1952; Gleason and Cronquist 1963). Too much variability is evident in the specimens examined, however, to permit a clear separation of this variant from var. *umbellatus*. Gray (1884) distinguished plants of var. *pubens* merely by

more copious pubescence on the lower leaf surface. Cronquist (1947), in his argument for species rank, considered additional characteristics, e.g., puberulent phyllaries and smaller heads (12–22 florets) compared with glabrous phyllaries and larger heads (23–54 florets) in *A. umbellatus* var. *umbellatus*. In applying these criteria, however, one may find that both taxa occur side by side in northern Illinois. I do not, therefore, recognize any varieties of this species for the flora of Illinois.

30. ***Aster undulatus*** L.
Wavy-leaved Aster



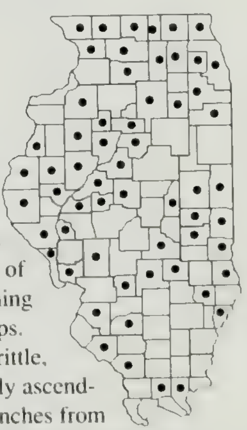
Herbaceous, with branched caudiciform rhizomes that turn woody with age but also sometimes with short stoloniform rhizome strands. **New shoots** arising at the base of old stems or from the rhizomes, the plants usually forming scattered individual clumps. **Stems** 1–several, erect, 40–120 cm tall, with ascending or divaricate branches above the middle, densely and uniformly hirtellous or villous on the upper stem portion and in the branches, somewhat pubescent in lines or glabrescent in the lower stem portion. **Leaves** polymorphic, the basal and lower cauline ones petiolate, those higher up on the stem subsessile or sessile and strongly clasping; upper surface of the blade mostly scabrous to hirsute (rarely glabrous), the lower surface hirtellous or loosely villous; leaves of new shoots and of the vernal rosettes with ovate-oblong to suborbiculate blades 1–6 cm long and 1–4 cm wide, purplish below, with two or more pairs of somewhat arching and anastomosing secondary nerves, the apex obtuse or rounded, the margins shallowly crenate-serrate to subentire, the base cordate or truncate to rounded, sometimes oblique, the petioles usually purplish, hirsute or pilose, winged, dilated, and sheathing at the base; principal cauline leaves variable in shape and size, gradually reduced upward on the stem, the lower ones petiolate, those higher up sessile and often constricted near or below the middle, the blades ovate to lanceolate in outline, 3–12(14) cm long and (1)2–5 cm wide, the secondary venation mostly obscured by indument, the apex acute to attenuate or acuminate and callus-pointed, the margins crenate-serrate or entire, and scabrous, the petioles progressively shorter and more broadly winged upward on the stem, conspicuously dilated toward the auriculate or cordate, clasping base; rameal leaves more or less abruptly reduced in size, oblong or lanceolate to linear-lanceolate, acute to attenuate, mucronulate, subentire to entire, sessile, slightly clasping or sheathing; leaves of the peduncles often numerous, firm, bracteiform, 2–3 mm long, appressed or ascending, intergrading with the phyllaries. **Capitulescence** paniculiform, often notably overtopping the leafy stem portion but also sometimes with branches arising from nodes near the middle of the stem, the ultimate head-bearing branchlets ascending or divaricate, often racemiform. **Flowering heads** 1.2–1.5(2) cm in diameter when the rays are fully extended, usually not crowded but sometimes secund, the peduncles 0.3–3(5) cm long, often densely bracteate, hirtellous. **Involucre** campanulate or hemispherical, 4–6(7) mm high, the phyllaries imbricated in 4 or 5(6) series. **Phyllaries** strongly graduated, appressed, or those of the outer series spreading, lanceolate, 1.5–2.5 mm long, the inner ones linear-oblanceolate, 4–5(6) mm long, puberulent on the abaxial surface and also thinly so on the adaxial surface, the green areoles rhombic or oblanceolate, the apex sharply acute, attenuate, or acuminate with somewhat inrolled margins, often mucronulate, the margins erose-hyaline, irregularly ciliolate, and with a scarious rim to near the tip, the basal $^1/_2$–$^2/_3$ portion scarious, or sometimes the midrib green to the base. **Receptacle** alveolate with mostly rounded teeth. **Ray florets** (12)15–25, the corollas 8–12 mm long, purple or blue, glabrous or nearly so. **Disk florets** 15–25, the corollas narrowly funnelform, (4)5–6 mm long, glabrous or with a few trichomes near the throat, the limb abruptly dilated at the throat, cream-colored or light yellow turning purple after anthesis, the lobe/limb fraction 0.2–0.25, the tube shorter than the limb. **Pappus** simple, the bristles about as long as the disk corolla or slightly shorter, cream-colored or slightly rose-tinged, soft, slender, and attenuate. **Achenes** oblong-obovoid, somewhat compressed, 2.5–3(3.5) mm long and 1.2–1.5 mm across, dull purple or light brown, sparsely puberulent at least

toward the top, with 4 or 5 straw-colored ribs. $2n = 32$; reported chromosome counts of $2n = 18$ and 36 are probably in error (A.G. Jones 1977, 1980b).

August–October. Dry or well-drained soils: loamy or rocky slopes at forest edges and open-wooded bluffs underlain by sandstone or limestone. Uncommon, restricted to the southern tip of the state; records from Jackson and Alexander counties mark the western limit for this extremely variable species. The range extends from NS and ME to c. FL, west to s. ON(?), OH, through s. IN, s. IL, and TN to c. MS and s.e. LA.

Aster undulatus has been included in the Illinois list of threatened species but is one of the more common asters in the mountains and woodlands to the east and southeast of our state. Although several varieties have been described, I am unable to assign Illinois populations to any of them. Even though the plants seem to differ somewhat from the type specimen of *A. undulatus*, I am treating them at this time *sensu lato* or as belonging in var. *undulatus*. There is evidence of occasional hybridization and intergradation with such closely related species as *A. drummondii* [e.g., *A.G. Jones 4089* (ILL) from Gallatin Co.] and *A. oolentangiensis* [e.g., *K. Wilson 3164* (ISM) from Pope Co.]. Collections that form the basis for *A. undulatus* sensu Mead (1846); Higley and Raddin (1891); Pepoon (1927); Kibbe (1952); and Dobbs (1963) non L. do not belong in this species.

31. *Aster urophyllus* Lindley in DC.



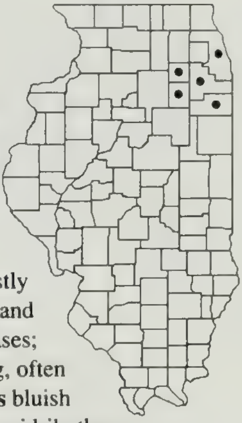
Herbaceous, with a stout caudiciform rhizome system lacking stoloniform strands. **New shoots** arising at or near the base of old stems, the plants forming scattered individual clumps. **Stems** 1–several, erect, brittle, 40–120 cm tall, with stiffly ascending, somewhat ridged branches from above the middle, sparsely puberulent in the upper portion and in the branches, the indument usually in decurrent lines (rarely uniformly distributed around the stem), the lower stem portion glabrescent or glabrous. **Leaves** polymorphic, the basal and larger cauline ones petiolate, those of the upper stem subsessile to sessile; leaves of new shoots and of the vernal rosettes with ovate or lanceolate blades 4–12 cm long and 2–5 cm wide, nearly glabrous, or often minutely scabrous above and thinly pubescent below, the secondary venation weakly expressed, the apex acute to acuminate, the margins shallowly crenate-serrate, the base cordate or truncate to rounded, the petioles 5–15 cm long, slender or narrowly winged, dilated, and sheathing at the base; principal cauline leaves gradually reduced in size upward on the stem, the blades ovate to lanceolate, 5–12 cm long and 2–5 cm wide, similar to the basal leaves in venation and vestiture, the apex acuminate to attenuate with a sharp, often purple callus point, the margins crenate-serrate to subentire, the base truncate or rounded, the petioles progressively shorter and more broadly winged upward on the stem, slightly sheathing; rameal leaves abruptly reduced in size, lanceolate to linear-lanceolate, glabrous or nearly so, attenuate and callus-pointed, entire, scabrous-margined, cuneate and slightly decurrent; leaves of the peduncles bracteiform, linear or subulate, 2–4 mm long, mostly ascending (rarely spreading to recurved), intergrading with the phyllaries. **Capitulescence** typically a dense, narrow, ovoid or pyramidal panicle in the upper 1/4–1/3(1/2) portion of the stem, commonly overtopping the leafy portion, the head-bearing branchlets stiffly ascending, often racemiform. **Flowering heads** 1–1.2(1.5) cm in diameter when the rays are fully extended, usually crowded and sometimes secund, subsessile or on often densely bracteate, puberulent peduncles 0.3–2 cm long. **Involucre** cylindrical or turbinate, 4.5–6(7) mm high, the phyllaries imbricated in 4 or 5 series. **Phyllaries** appressed or somewhat recurved-spreading, graduated, the outer subulate, 2–3 mm long, the inner linear-lanceolate, 5–6(7) mm long, glabrous, scarious over most of the surface area, the light green areoles very slender, linear to linear-oblanceolate, the apex long-attenuate, terminating in an often recurved, spinulose mucro, the margins erose-hyaline and irregularly ciliolate. **Receptacle** alveolate with sharp teeth. **Ray florets** (8)10–12(14), the corollas 6–8(10) mm long, typically white (rarely lavender), sparsely

puberulent on the tube and throat. **Disk florets** 10–15, the corollas funnelform, abruptly dilated, (3.5)4–5 mm long, glabrous or with a few trichomes near the throat, the limb cream-colored turning pinkish after anthesis, the lobe/limb fraction 0.2–0.25, the tube much shorter than the limb. **Pappus** simple, the bristles shorter than the disk corolla, whitish or slightly discolored to rose-tinged, soft, slender, and attenuate. **Achenes** oblong-obovoid, somewhat compressed, 1.8–2.5 mm long and ca 1 mm across, dull purple or brown, glabrous, with 4 or 5 ribs. $2n = 16$. [*A. sagittifolius* sensu auct. (pro parte) non Wedem. ex Willd. (see A.G. Jones 1980b; Jones and Hiepko 1981). *A. hirtellus* Lindley in DC. *A.sagittifolius* var. *hirtellus* (Lindley in DC.) Burgess in Britton & Brown f. *hirtellus* (Lindley in DC.) Shinners (1941)—Steyermark 1963. *A. sagittifolius* var. *urophyllus* (Lindley in DC.) Burgess in Britton & Brown—Deam 1940. *A. cordifolius* var. *moratus* sensu Fern. (1950) non (Shinners) Shinners.]

August–October. Loamy or rocky soils in dry or mesic situations: woodland edges, open upland woods, and thickets, also in disturbed ground of pastures, roadsides, and railroad rights-of-way. Common throughout much of the state. The range extends in the East from s.e. Canada and ME south to GA, AL, and n. FL, and in the West from MN through IA, MO, and s.e. NE to s.e. KS, with scattered stations recorded from AR and MS.

Description of *Brachyactis* Species

Brachyactis ciliata (Ledeb.) Ledeb.
Rayless Aster



Taprooted and somewhat succulent annual. **Stem** erect, 10–70 cm tall, bluish or yellowish green, often red-tinged, glabrous or with a few bristly trichomes in the leaf axils and along the decurrent leaf bases; branches mostly ascending, often from near the base. **Leaves** bluish green, with a conspicuous midrib, the secondary venation faintly expressed; basal leaves spatulate, soon withered; principal cauline leaves linear, 3–10 cm long and 0.1–0.9 cm wide, gradually reduced in size upward on the stem, sessile, with clusters of smaller leaves produced in the axils, glabrous, the apex acute to short-attenuate, the margins entire and appressed ciliate, the base slightly dilated and sheathing; rameal leaves similar in contour, those of the peduncles few. **Capitulescence** a contracted panicle, or racemiform in poorly developed plants. **Heads** several to many, short-peduncled or subsessile. **Involucre** 6–10 mm high, the phyllaries imbricated in 3 or 4 series. **Phyllaries** subequal or somewhat graduated, occasionally those of the outer series longer than those of the middle and inner series, glabrous, linear to oblanceolate, (4)5–8 mm long, the outer and median ones herbaceous except for a narrow scarious margin, the apex acute or obtuse and mucronulate. **Receptacle** flat, shallowly alveolate with rounded teeth, or merely pitted in fruiting heads. **Florets** 40–80 (or more). **Pistillate florets** fertile, in several series, usually more numerous than the disk florets, the corollas slender, tubular, with a long-exserted pink style and no stamens; rays (ligules) absent or rudimentary. **Disk florets** perfect and fertile, the corollas tubular or narrowly funnelform, 3–4.5 mm long, the limb whitish aging to pink, with 5 very short lobes, the tube slender, yellowish green, longer than the limb. **Style branches** of the disk florets with attenuate, papillate, sterile appendages that are longer than the stigmatic lines. **Pappus** very prominent, considerably overtopping the corolla, the capillary bristles numerous, in 2 or 3 series, pure white or faintly pink, subequal in length, 4–6 mm long, soft and silky, attenuate, and minutely barbellate. **Achenes** oblong-obovoid, slender, slightly compressed, 1.5–2.5 mm long and 0.4–0.5 mm across, gray or whitish, often with purple streaks, pilose or strigillose, obscurely 2–4 ribbed. $2n = 14$. Including *B. angusta* (Lindley in Hooker) Britton in Britton & Brown (see A.G. Jones 1984). [*Aster brachyactis* S.F. Blake—G.N. Jones 1945, 1950, 1963; Jones and Fuller 1955; Swink 1974; Mohlenbrock 1975, 1986; Swink and Wilhelm 1979; and others.]

August–October. Disturbed ground: waste places, roadsides and railroad tracks. Occasional, recorded from only five counties of the Chicago region; adventive from the North and the West. The species range extends from NT and James Bay, ON, east to PQ, PE, and NB, and west through the northern half of the Great Plains to n. WA; the plants were also recorded from scattered stations in s.e. WI, n. IA, w. MO, w. NE, w. KS, w. OK, and s. and e. CO.

The species was originally described (under the name *Erigeron ciliatus* Ledeb.) from collections made in Siberia. North American plants may be recognized as *Brachyactis ciliata* subsp. *angusta* (Lindley in Hooker) A.G. Jones [based on *Tripolium angustum* Lindley in Hooker. *Aster angustus* (Lindley in Hooker) Torrey & Gray non Nees—Pepoon 1927. *B. angusta*—Hill 1902]. This taxon, however, can probably not be distinguished from typical subsp. *ciliata* on any basis other than geography.

Brachyactis is a small genus of two or three species with the center of distribution probably in North America. The genus can be distinguished from *Aster* and other members of the Astereae by a combination of the following: pistillate florets that lack or have inconspicuous ray corollas, a prominent pappus that considerably overtops the disk corollas and is composed of numerous subequal bristles in several series, and the uncommon basic chromosome number of $x = 7$. Most authors retain the taxon as a section of *Aster* (cf. Houle and Brouillet 1985; Semple and Brouillet 1980a, b).

Glossary of Descriptive Terms

abaxial side of an organ away from the axis
achene dry, indehiscent, one-seeded fruit
aciculiform needle-shaped
acuminate tapering more or less abruptly to a slender sharp point, the margins somewhat curved inward
acute terminating in a sharp point at an angle of between 45° and 90°, the margins straight (see also **attenuate**)
adaxial side of an organ facing the axis
adventive introduced from an adjacent or nearby region and spreading in the new region
alveolate honeycombed
anastomosing veins (or nerves) connected by cross veins (or nerves)
anthesis flowering time, i.e., period during which pollination takes place
apex; apical tip; pertaining to the tip
areole small space clearly marked out on a surface
ascending directed upward after arising at an oblique angle or on a curve
attenuate gradually tapering to a narrow and slender tip at an angle of less than 45°, the margins more or less straight (see also **acute**)
auriculate having auricles, i.e., with ear-shaped appendages
barbellate with minute barbs
bracteate having bracts
bracteiform bractlike
bulliform appearing blistered, bubblelike
callus a hard protuberance or thickening
campanulate bell-shaped
capitulescence cluster (often a large assemblage) of flower heads (commonly synonymized with inflorescence)
caudex the usually condensed, thick, tough, persistent, largely underground base of an otherwise herbaceous stem
caudiciform stem base shaped like a caudex, i.e., condensed, thick, and tough
cauline pertaining to or arising from the stem
cespitose growing in tufts, e.g., several stems from a common base
ciliate fringed with slender trichomes (see also **fimbriate**)
ciliolate minutely ciliate, i.e., the trichomes short
cinereous with ash-colored (light gray) indument
clasping the base of a leaf or petiole nearly or completely surrounding the stem
clavellate minutely club-shaped, i.e., expanded toward the apex
cordate heart-shaped, the base with rounded lobes and a sinus
corolla perianth whorl composed of petals (united in the Asteraceae)
corymbiform shaped like a corymb, i.e., a flat-topped capitulescence with the lower (outer) branchlets and peduncles longer than the upper (inner) ones
crenate toothed with rounded teeth
cuneate wedge-shaped with the narrow end at the point of attachment
cymiform shaped like a cyme, i.e., resembling an inflorescence in which the central or terminal flower opens first
cymule a small few-flowered cyme; refers in the Asteraceae to an ultimate cluster of the cymiform capitulescence
deciduous falling off at maturity or after withering
decumbent reclining on the ground but with the tips ascending
decurrent pertaining to leaf bases or veins that continue downward from the nodes in the form of wings, ribs, or lines of indument
dichotomous forked with two nearly equal branches
dilated expanded in width or widened in diameter
disk floret flower of the central portion of a head, the corolla regular, 5-lobed
divaricate spreading at a wide angle
erose with the margin appearing eroded or gnawed
falcate sickle-shaped
fastigiate with the branches partway parallel and close together; broomlike
filament the stalk portion of a stamen that supports the anther
fimbriate fringed with coarse trichomes or processes (see also **ciliate**)
foliaceous leaflike or leafy
funnelform resembling or shaped somewhat like a funnel
fusiform spindle-shaped, swollen near the middle and tapering at both ends
glabrescent nearly glabrous or becoming glabrous

glabrous smooth, i.e., without vestiture

glandular invested with glands, i.e., with structures that produce a viscid sap

glaucous covered with a waxy, bluish bloom that often rubs off easily

habit general appearance

head capitulum = unit of capitulescence (the individual florets sessile)

hirsute having coarse or stiff, spreading or ascending trichomes

hirtellous minutely hirsute, i.e., with short, spreading trichomes

hispid having rigid spreading bristles or spinules

hispidulous minutely hispid

hyaline translucent or colorless

imbricated overlapping, i.e., shinglelike in a spiral arrangement

indument hairy covering

indurate hardened

inrolled rolled inward or downward at the edges

involucre one or more series of bracts (phyllaries) subtending the florets of a head (in the Asteraceae)

isodiametric with all the diameters of an areole about equal in length

keel; keeled a central abaxial ridge formed by the midrib of a compressed phyllary, bract, or leaf; forming a keel

lanate woolly, with long, tangled, curly trichomes

lanceolate lance-shaped; much longer than broad, widest near the base and tapering to the apex

ligule the strap-shaped limb of a ray floret in the Asteraceae

limb upper, expanded portion of a corolla (in disk florets, the portion above the zone of attachment of the filaments) as distinct from the tube portion

mucro a sharp, short, and abruptly narrowed point or protuberance

mucronate tipped with a mucro

mucronulate diminutive of mucronate

node the place on the stem where leaves are attached and branches arise

ob- Latin prefix meaning inverted, e.g., obovate = inverse of ovate

oblique slanting, not straight up, or at an angle that is not 90°

oblong at least two times longer than broad with nearly parallel sides

obtuse blunt; if sharp-pointed, with an angle of more than 90°

ovate; ovoid egg-shaped, with the broader part near the base

panicle a variously branched compound inflorescence (in the Asteraceae a compound capitulescence with pedunculate flower heads)

paniculiform resembling or shaped like a panicle

papillate nipplelike

pappus the specialized outer perianth whorl in the Asteraceae composed of bristles (in *Aster*), awns, or scales

peduncle the stalk of a head

perfect having both functional stamens and pistils

petiole; petiolate the stalk of a leaf; having a stalk

phyllary bract of the involucre

pilose invested with long, soft, slender trichomes

pinnate arising from both sides of the axis or midrib

pistillate having pistils but no functional stamens

polymorphic exhibiting several forms (morphs) of the same organ

pro parte in part

pro sp. described as a species

puberulent minutely or finely hairy

pubescence; pubescent hairiness; hairy

pulvinate swollen or cushion-shaped

puncticulate having minute colored or translucent dots

pustulate with pimplelike or blisterlike raised areas

racemiform resembling or shaped like a raceme, i.e., an elongate capitulescence or branch with pedunculate heads

rameal of or pertaining to the branches

ray floret of the outer series of florets in a head, the corolla strap-shaped (= ligulate)

receptacle the expanded end of the peduncle, i.e., the end bearing the aggregate of florets

reflexed abruptly bent or turned downward

remote distantly spaced

reticulate; reticulum interconnected like a network

rhizome an elongate, often branched underground stem, usually with minute scale leaves and rooting at or producing new shoots from the nodes

rhombic shaped like a rhombus, i.e., like an equilateral, oblique-angled parallelogram; more or less diamond-shaped
rosette a cluster of leaves with very short internodes, arranged in a compact, spiral (near-circular) series
rugose; rugulose wrinkled
scabrellous minutely scabrous
scabrous rough to the touch, the stiff trichomes pointing in one direction
scarious thin, dry, membranous, not green
secund directed to one side of the stem or branchlet
sensu auct. according to author(s)
sensu lato in a broad sense
sensu stricto in a narrow sense
sericeous silky, with appressed, soft, glossy trichomes
serrate with sharp teeth that point forward
serrulate finely serrate
sessile lacking a stalk
sheathing closely enveloping
spatulate spatula-shaped or spoon-shaped
spiciform shaped like a spike, i.e., a simple, elongate capitulescence with sessile heads
spinule; spinulose short spine; minutely spiny
squarrose having the parts recurved at the tip (mostly applied to phyllaries)
stamen pollen-bearing organ
stigmatic pertaining to the portion of the style branches receptive to pollen
stoloniform shaped like stolons (applied to long-creeping horizontal rhizomes)
striate marked with fine longitudinal lines or ridges
strigillose minutely strigose, i.e., the trichomes very short
strigose with the trichomes appressed and lined up in one direction
style the elongated part of the pistil above the ovary
subulate awl-shaped; slender, tapering to a sharp point
suffruticose plants woody only at the base and herbaceous over most of the above-ground portion
terete circular in cross section
throat expanding zone in a corolla at the junction of tube and limb
thyrsiform shaped like a thyrse, i.e., like a compact or contracted panicle
tomentose invested with short-haired, matted, woolly pubescence
trichome an epidermal structure (hair, bristle, or prickle)
truncate ending abruptly as if cut off
turbinate top-shaped, i.e., inversely conical
umbelliform resembling or shaped like an umbel, i.e., a flat-topped capitulescence in which several peduncles more or less arise from a common point
urceolate urn-shaped, e.g., a corolla that is abruptly contracted just below the mouth
vestiture any covering of the surface, i.e., indument and/or glands
villous woolly, the trichomes long, soft, and curly but not matted or tangled

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Index to Scientific Species Names, Including Synonyms

The names of accepted Illinois species are given in roman type. Bold-faced page numbers indicate species descriptions.

Index to Vernacular (Common) Names

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(Mycota-Ascomycotina-Loculoascomycetes)

J.L. Crane and C.A. Shearer

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Introduction and Historical Background

This nomenclator of *Leptosphaeria* is an index to names published in the genus through 1989 and includes the source of publication, nomenclatural history, substrate and/or host, and geographical location for each species name. Orthographic errors of specific epithets were corrected, with the original spelling given in brackets. Full names and initials of authorities are given. Standardized, complete names of periodicals are cited following the system of Brown and Stratton (1963), Porter and Koster (1970), Koster and Gascoigne (1971), and Smits (1968). The titles of books and pamphlets are cited according to Stafleu and Cowan (1976–1988). Obligate synonomy is indicated by the symbol ≡. Articles of the International Code of Botanical Nomenclature cited in this work follow Greuter et al. (1988). Several authors have described new species in *Leptosphaeria* as trinomials in which the subgenus or group to which the new species belongs is indicated as a middle name in parentheses; an example is *Leptosphaeria* (*Clypeosphaeria*) *hendersoniae*. Such trinomials are alphabetized by specific epithet; however, the group name precedes the epithet.

The scientific names of host plants are given as reported in the protologue of each *Leptosphaeria* species, with the currently accepted name in parentheses. Several host epithets reported in the original descriptions were never published or could not be verified. These are changed to "sp." Plant host families and genera were verified in Willis (1973), Farr et al. (1979), and Cronquist (1981). Specific epithets of vascular plants were confirmed in Halliday and Beadle (1983), Kartesz and Kartesz (1980), the Gray Herbarium Card Index (1894–present), and Index Kewensis (1895–present). Names of pteridophytes were substantiated in Christensen (1905–1906), and names of mosses, in Wijk et al. (1959–1960). Lichenized fungi names follow Zahlbruckner (1921–1940) and Lamb (1963), and fungal host names were verified in Saccardo (1882–1931) and the Index of Fungi (1920–1987). For convenience, *Leptosphaeria* species reported from Algae, Fungi, Lichenes, and Musci are listed under these headings and their respective hosts in the host index. When available, specific substrate information, such as leaf, stem, water, etc., is given.

The geographical location of species is usually described by country and is based on information in the protologue and new combinations. Geographical names were verified in Seltzer (1952).

Cesati and de Notaris (1863) established the genus *Leptosphaeria* and included 26 species; among these was *Leptosphaeria hirta* (G.L. Rabenhorst) V. Cesati & G. de Notaris, the type species of an earlier genus, *Nodulosphaeria* G.L. Rabenhorst, 1858. *Leptosphaeria* was conserved against *Nodulosphaeria* with *Leptosphaeria doliolum* (C.H. Persoon:E.M. Fries) V. Cesati & G. de Notaris as the type species (Greuter et al. 1988). The original description of *Leptosphaeria* was superficial by modern taxonomic standards, and the genus was delimited largely by ascospore characteristics. The ascospore characteristics selected (oblong or fusoid, two- to many-celled, hyaline, becoming yellowish or dark brown) and the poor characterization of other structural features resulted in the inclusion of a wide range of Ascomycetes in this genus. *Leptosphaeria* now comprises approximately 1,689 taxa. These taxa represent, according to present-day concepts of ascomycete classification, a melange of Euascomycetes and Loculoascomycetes.

Few mycologists have attempted to deal with the systematics of *Leptosphaeria*. Saccardo (1878, 1883, 1891, 1895, 1899, 1913, 1928) recognized 800 species, which he grouped primarily according to host (parasites of dicotyledons, monocotyledons, and cryptogams) and habit (species on stems and/or branches and leaves). Species were further subdivided, based on the external features of

the pseudothecium (glabrous, hairy, setose) and ascospore septation. Saccardo's concept of *Leptosphaeria* was broad, and his emended description specified the presence of pseudoparaphyses (as paraphyses).

Höhnel (1907a) was the first to use information on centrum structure for the classification of *Leptosphaeria*-like fungi. He established the family Pseudosphaeriaceae for species in which the asci grow up into a cellular tissue that occupies the inner space of the fruiting body. As the asci develop, the cellular tissue becomes compressed and at fruiting-body maturity simulates paraphyses similar to those found in the Sordariales (Pyrenomycetes). In the Sordariales, however, the paraphyses originate prior to the asci, and the asci grow up among them. Höhnel included four genera in the Pseudosphaeriaceae [*Pseudosphaeria* F. v. Höhnel, *Pyrenophora* F. v. Höhnel, *Scleroplea* (P.A. Saccardo) C.A. Oudemans, and *Wettsteinina* F. v. Höhnel]. Later, Höhnel (1918a, 1918b) divided *Leptosphaeria* into three genera based on centrum structure (*Leptosphaeria*, *Scleropleella* F. v. Höhnel, and *Nodulosphaeria* G.L. Rabenhorst) (Appendix 1). Petrak (1923) subsequently provided evidence that *Leptosphaeria* is related to *Wettsteinina* and belongs in the Pseudosphaeriaceae.

Wehmeyer (1942) reported the occurrence of 13 species of *Leptosphaeria* from North America and described two new species. He noted, "Many of the species show minor differences of spore structure, often correlated with the host. In the descriptive literature, these details are not always given. Large numbers of species have been described, largely on host distinction, on the one hand, whereas many host varieties have been obscured by inclusion in one of the ubiquitous species on the other hand. As a result it is difficult to be sure of species determinations without a comparative study of the entire genus." This statement remains valid today. Wehmeyer (1946) also redescribed seven species of *Leptosphaeria* and discussed evolutionary trends within the genus. He noted that 382 species have the 3-septate type of ascospore and believed that the 3-septate, dark brown spore type is the primitive state. According to Wehmeyer, the spores of more recently evolved species are lighter in color, longer, narrower, and more septate. These trends lead directly, without a break, to *Ophiobolus* H. Riess.

Müller (1950), circumscribing *Leptosphaeria* broadly, considered 114 species occurring in Switzerland. Within his broad generic concept, Müller divided *Leptosphaeria* into four sections (Appendix 1). These sections were circumscribed based on pseudothecial and centrum structure and ascospore morphology. Three of his sections correspond, in part, to the three groups of Höhnel (Appendix 1).

Munk (1957) accepted Müller's sections with certain reservations and divided *Leptosphaeria* into four somewhat different sections (Appendix 1). Sections I (*Eu-Leptosphaeria*), III (*Scleropleella*), and IV (*Nodulosphaeria*)—which correspond to Müller's Sections II, I, and IV, respectively—were more restricted than those of Müller. The remaining species of *Leptosphaeria* were treated in Section II (*Para-Leptosphaeria*).

Holm (1957), in a treatment of 62 Swedish species of *Leptosphaeria*, rejected Müller's broad concept of *Leptosphaeria* and limited the genus to those species most closely related to *Leptosphaeria doliolum*, the type of the genus (Appendix 1). Excluded species were distributed primarily in *Nodulosphaeria* H. Riess, *Phaeosphaeria* I. Miyake, and *Entodesmium* H. Riess. Holm placed much emphasis on substrata and relation of the pseudothecium to the substratum. Holm's disbursement of *Leptosphaeria* species was rejected by both Dennis (1978) and Sivanesan (1984) but was accepted by Hedjaroude (1969), v. Arx and Müller (1975), Eriksson (1967), and Shoemaker (1984).

In the past 50 years, there have been a large number of intergeneric transfers of *Leptosphaeria* species. Many of these transfers have come about by the partitioning of species groups into new (*Paraphaeosphaeria* O. Eriksson) or existing (*Entodesmium* H. Riess and *Phaeosphaeria* I. Miyake) genera. Other species have been transferred to genera very similar to and integrating with *Leptosphaeria* (*Lidophia* J.C. Walker & B.C. Sutton, *Massaria* G. de Notaris, *Massarina* P.A. Saccardo, *Melanomma* T.R.J. Nitschke ex L. Fuckel, *Ophiobolus* H. Riess, and *Wettsteinina* F. v. Höhnel). Descriptions of related genera and a synopsis of their relationships to *Leptosphaeria*

are summarized in Appendix 2. Genera synonymous with *Leptosphaeria* are listed in Appendix 3.

In recent years, *Leptosphaeria* has been included in two orders in the Bitunicatae or Loculoascomycetes. Luttrell (1973) placed *Leptosphaeria* in the Pleosporales under the Pleosporaceae. Von Arx and Müller (1975) retained *Leptosphaeria* in the Pleosporaceae under the Dothideales. Hawksworth et al. (1983) placed *Leptosphaeria* in the Dothideales in either the Phaeosphaeriaceae or the Pleosporaceae. Eriksson and Hawksworth (1986) classified the genus in Dothideales under Phaeosphaeriaceae. Most recently, Barr (1987a) has placed *Leptosphaeria* in the Leptosphaeriaceae of the Pleosporales in the Loculoascomycetes.

One of the most intriguing aspects of *Leptosphaeria* is the diversity of anamorphic states attributed to this genus. Anamorphs of *Leptosphaeria* have been demonstrated for 70 species, and most of these associated anamorphs are Coelomycetes (Appendix 4). The largest numbers of *Leptosphaeria* associations are with *Phoma* P.A. Saccardo and *Stagonospora* (P.A. Saccardo) P.A. Saccardo.

It is intended that this nomenclator will be the base for a reappraisal of *Leptosphaeria* using modern concepts and techniques applicable to Loculoascomycetes.

List of *Leptosphaeria* Species, Varieties, and Forms

abbreviata (M.C. Cooke) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:26. 1883. ≡*Sphaeria abbreviata* M.C. Cooke, Handbook of British Fungi, p. 893. 1871. On dead stems of *Rubus* sp., Rosaceae. Great Britain.

abuensis K.S. Panwar & S.J. Kaur, Kavaka, Madras 3:67–68. 1975. On dead wood of unknown host, unknown family. India.

abutilonis M. Chochrjakov *in* V. Tranzschel, L. Gutner, and M. Chochrjakov, Trudȳ Instituta Novogo Lubyanogo Sȳr'ya, Moskva 4:133. 1933. On leaves of *Abutilon avicennae* Gaertner, Malvaceae. U.S.S.R.

abutilonis L.E. Wehmeyer & S. Ahmad, Biologia. Biological Society of Pakistan, Lahore 10:12. 1964. Nom. illegit. Art. 64.1. On unknown substrate of *Abutilon indicum* (L.) Sweet, Malvaceae. Pakistan.

acanthi N.T. Patouillard, Revue Mycologique, Toulouse 8:181. 1886. On dead stems of *Adhatoda* sp., Acanthaceae. China.

aceris N.N. Woronichin, Vestnik Tiflisskogo Botanicheskogo Sada, Tiflis (Moniteur du Jardin Botanique de Tiflis) 35:5. 1914. On living leaves of *Acer laetum* C.A. Mey., Aceraceae. U.S.S.R. (Caucasus).

acheniarum K. Starbäck [see *Leptosphaeria agnita* var. *acheniarum* K. Starbäck].

achilleae (B. Auerswald) V. Cesati & G. de Notaris, Commentario della Società Crittogamologica Italiana, Milan 1:236. 1863. ≡*Sphaeria achilleae* B. Auerswald *in* G.L. Rabenhorst, Klotzschii Herbarium Vivum Mycologicum Sistens Fungorum Per Totam Germaniam Cresentium Collectionem Perfectam, Dresden, Edition 1, Century 15, No. 1448. Anno 1850. On stems of *Achillea millefolium* auct., Compositae. Germany.

acicola (L. Fuckel) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:55. 1883. ≡*Pleospora? acicola* L. Fuckel, Symbolae Mycologicae, Erster Nachtrag, p. 301. 1871. On fallen needles of *Pinus sylvestris* L., Pinaceae. Germany.

aconiti P.A. Saccardo, Nuovo Giornale Botanico Italiano e Bolletino della Società Botanica Italiana, Firenze 7:315. 1875. On dry stems of *Aconitum napellus* L., Ranunculaceae. Italy.

(*Metasphaeria*) *acorella* M.C. Cooke, Grevillea, London 13:99. 1885. ≡*Metasphaeria acorella* (M.C. Cooke) A.N. Berlese & P. Voglino, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo Additamenta Ad Volumina I–IV, p. 158. 1886. On leaves of *Acorus calamus* L., Araceae. Great Britain.

acori P.A. Karsten, Hedwigia, Dresden 22:179. 1883. [Ad interim.] Nom. inval. Art. 34.1. On decaying leaves of *Acorus calamus* L., Araceae. Finland.

aculeorum G. Passerini, Atti della R. Accademia dei Lincei Memoriae, Rome, Series 4, 6:458–459. (1889) 1890. On stems of *Rosa canina* L., Rosaceae. Italy.

acuta H. Rehm, Ascomyceten, Fascicle 16, No. 783. Anno 1884. Nom. illegit. Art. 64.1. ≡*Leptosphaeria acutiuscula* A.N. Berlese.

acuta (G.F. Hoffmann:E.M. Fries) P.A. Karsten, Mycologia Fennica Pars 2, Pyrenomycetes, p. 98. 1873. ≡*Sphaeria acuta* G.F. Hoffmann:E.M. Fries, Vegetabilia Cryptogama, Fascicle 1, p. 22. 1787; E.M. Fries, Systema Mycologicum Sistens Fungorum 2:507. 1823. ≡*Pleospora acuta* (G.F. Hoffmann:E.M. Fries) L. Fuckel, Symbolae Mycologicae, p. 135. 1870. ≡*Ampullina acuta* (G.F. Hoffmann:E.M. Fries) L. Quélet, Mémoires de la Société d'Émulation de Montbéliard, Series 2, No. 5, pp. 523–524. 1875; Les Champignons du Jura et des Vosges 3:95. 1875. On fallen stems of *Urtica dioica* L., Urticaceae. Austria, Belgium, Finland, France, Germany, Great Britain, Italy, U.S.A.

acuta (G.F. Hoffmann:E.M. Fries) P.A. Karsten forma *insignis* F. Fautrey *in* C. Roumeguère, Fungi Selecti Gallici Exsiccati, Century 72, No. 7137. Anno 1897; Revue Mycologique, Toulouse 19:149. 1897. On dry, decorticated stems of *Urtica dioica* L., Urticaceae. France.

acuta (G.F. Hoffmann:E.M. Fries) P.A. Karsten forma *urticae* F. Fautrey *in* C. Roumeguère, Revue Mycologique, Toulouse 16:7. 1894;

Fungi Selecti Gallici Exsiccati, Century 65, No. 6434. Anno 1894. On diseased stalks of *Urtica dioica* L., Urticaceae. France.

acutispora S. Tóth, Omagiu Lui Traian Săvulescu cu Prilejul Implinirii A 70 De Ani, Academia Republicii Populare Romane, Bucharest, p. 778. 1959. On dry stems of *Erysimum diffusum* Ehrh., *Erysimum erysimoides* (L.) Fritsch ex Janchen, *Sisymbrium strictissimum* L., Cruciferae. Romania.

acutiuscula A.N. Berlese, Icones Fungorum Omnium Hucusque Cognitorum ad usum Sylloges Saccardianae Adcommodatae 1:86. 1894. ≡*Leptosphaeria acuta* H. Rehm. On stems of *Urtica* sp., Urticaceae. Germany.

adesmicola (C.L. Spegazzini) L. Holm, Svensk Botanisk Tidskrift, Stockholm 62:224–225. 1968. ≡*Gibberidea adesmicola* C.L. Spegazzini, Anales del Museo Nacional de Historia Natural de Buenos Aires 19(Series 3, 12):385. 1909. On dead branches of *Adesmia* sp., Leguminosae. Argentina.

advenula (W. Nylander) P.A. Saccardo & D. Saccardo *in* P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 17:731. 1905. On thallus of *Lecidea excentrica* Roehling, Lichenes (Lecideaceae). Ireland, Italy.

aegira P.A. Saccardo & C.L. Spegazzini *in* P.A. Saccardo, Michelia Commentarium Mycologicum Fungos in Primis Italicos Illustrans 1:37. 1877. On wilting leaves of *Populus alba* L., Salicaceae. Italy.

aeluropodis A.I. Lobik, Materialȳ po Floristicheskim i Faunisticheskim Obsledovaniyam Terskogo Okruga, pp. 22–23. 1928 [as *aeluropi*]. On leaves of *Aeluropus littoralis* (Gouan.) Parl., Gramineae. U.S.S.R.

aerea C.L. Spegazzini, Anales de la Sociedad Cientifica Argentina, Buenos Aires 12:178–179. 1881. Fungi Argentini Pugillus 4, No. 166. 1881. ≡*Sphaerulina (Leptosphaerella) aerea* (C.L. Spegazzini) M.C. Cooke, Grevillea, London 18:80. 1890. =*Pleospora pellita* (E.M. Fries) G.L. Rabenhorst var. *pellita*, fide L.E. Wehmeyer, A World Monograph of *Pleospora*, p. 47. 1961. On branches and dead leaves of *Erythrina crista-galli* L., *Tillandsia bicolor* Brongn., Leguminosae, Bromeliaceae. Argentina.

aetnensis G. Scalia, Prima Contribuzione alla Conoscenza delle Flora Micologica della Provincia di Catania, p. 16. 1899. On dry branches of *Smilax aspera* L., Smilacaceae. Italy.

affinis P.A. Karsten, Fungi Fenniae Exsiccati, Century 9, No. 896. Anno 1869. ≡*Metasphaeria affinis* (P.A. Karsten) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Diggesit P.A. Saccardo 2:159. 1883. On dead stems of *Rhinanthus* sp., Scrophulariaceae. Finland.

africana A.M. Saccas, Étude de la Flore Crytogamique des Caféiers en Afrique Centrale. Bulletin de Institut Français du Café du Cacao et d'Autres Plantes Stimulantes (Bulletin IFCC No. 16), pp. 219–221. 1981. Nom. inval. Art. 37.1. On dead branches of *Coffea robusta* L. Linden (=*Coffea canephora* Pierre ex Froehn.), Rubiaceae. South Africa.

agaves H. Sydow, P. Sydow, & E.J. Butler, Annales Mycologici, Berlin 9:409. 1911. On wilted leaves of *Agave rigida* Mill. var. *sisalana* (Perrine) Engelm., Agavaceae. India.

aglaja P.A. Saccardo, Nuovo Giornale Botanico Italiano e Bolletino della Società Botanica Italiana, Firenze 7:310. 1875. On leaves of *Oxalis stricta* L., Oxalidaceae. Italy.

agminalis P.A. Saccardo & P. Morthier *in* P.A. Saccardo, Michelia Commentarium Mycologicum Fungos in Primis Italicos Illustrans 1:498–499. 1879. ≡*Dothideopsella agminalis* (P.A. Saccardo & P. Morthier) F. v. Höhnel, Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-naturwissenschaftliche Klasse, Abt. I, 124(1 & 2):70. 1915. On stems of *Clematis vitalba* L., Ranunculaceae. France, Italy.

agminalis P.A. Saccardo & P. Morthier forma *minor* F. Fautrey *in* C. Roumeguère, Revue Mycologique, Toulouse 13:168. 1891; Fungi Selecti Gallici Exsiccati, Century 59, No. 5849. Anno 1891. On unknown substrate of *Clematis vitalba* L., Ranunculaceae. France.

agnita (J. Desmazières) V. Cesati & G. de Notaris, Commentario della Società Crittogamologica Italiana, Milan 1:236. 1863. ≡*Sphaeria (Caulicola) agnita* J. Desmazières, Annales des Sciences Naturelles, Paris, Botanique, Series 3, 16:313. 1851. On stems of *Valeriana officinalis* L., Valerianaceae. Italy.

agnita (J. Desmazières) V. Cesati & G. de Notaris subsp. *labens* P.A. Saccardo & G. Scalia *in* P.A. Saccardo, C.H. Peck, and W. Trelease. Harriman Alaska Expedition 5:330. 1904. On dead herbaceous stems of unknown host. U.S.A.

agnita (J. Desmazières) V. Cesati & G. de Notaris var. *acheniarum* K. Starbäck, Arkiv för Botanik, Uppsala, Stockholm 5(7):23. 1905. [Raised to species rank; *Leptosphaeria acheniarum* K. Starbäck in reprint on same page.] On dry achenes of *Mikania* sp., Compositae. Bolivia.

agnita P.A. Saccardo var. *ambigua* A.N. Berlese, Atti dell' Accademia Scientifica Veneto-Trentino-Istriana, Padova, Series 1, 9:247–248. 1886; Ricerche intorno alla *Leptosphaeria agnita* (Desm.) Ces. et de Not., ed alla *L. ogilviensis* (B. et Br.) Ces. et de

Not., pp. 4–5. 1886. On dry stems of *Eupatorium cannabinum* L., Compositae. Germany.

agnita (J. Desmazières) V. Cesati & G. de Notaris var. *bupleuri* P.A. Saccardo, Bulletin. Société R. de Botanique de Belgique, Bruxelles 28:91. 1889. On dead stems of *Bupleurum falcatum* L., Umbelliferae. U.S.S.R.

agnita P.A. Saccardo var. *chrysanthemi* A.N. Berlese, Atti dell' Accademia Scientifica Veneto-Trentino-Istriana, Padova, Series 1, 9:246–247. 1886; Ricerche intorno alla *Leptosphaeria agnita* (Desm.) Ces. et de Not., ed alla *Leptosphaeria ogilviensis* (B. et Br.) Ces. et de Not., pp. 3–4. 1886. On dry stems of *Chrysanthemum corymbosum* L., Compositae. Germany.

agnita (J. Desmazières) V. Cesati & G. de Notaris var. *erigerontis* A.N. Berlese, Atti dell' Accademia Scientifica Veneto-Trentino-Istriana, Padova, Series 1, 9:247. 1886; Ricerche intorno alla *Leptosphaeria agnita* (Desm.) Ces. et de Not., ed alla *Leptosphaeria ogilviensis* (B. et Br.) Ces. et de Not., p. 4. 1886. On dead stems of *Erigeron canadensis* L., Compositae. U.S.A.

agnita (J. Desmazières) V. Cesati & G. de Notaris var. *major* P.A. Saccardo & A.N. Berlese, Atti del Istituto Veneto di Scienze, Lettere ed Arti, Venezia, Series 6, 3:730. 1885. On stems of *Chaerophyllum aureum* L., Umbelliferae. Switzerland.

agnita P.A. Saccardo var. *major* A.N. Berlese, Atti dell' Accademia Scientifica Veneto-Trentino-Istriana, Padova, Series 1, 9:247. 1886; Ricerche intorno alla *Leptosphaeria agnita* (Desm.) Ces. et de Not. ed alla *Leptosphaeria ogilviensis* (B. et Br.) Ces. et de Not., p. 4. 1886. On dry stems of *Chaerophyllum aureum* L., Umbelliferae. Germany.

agnita (J. Desmazières) V. Cesati & G. de Notaris var. *trifolii* R. González Fragoso, Memórias de la R. Sociedad Española de Historia Natural, Madrid 11:90. 1919. On dry stems of *Trifolium angustifolium* L., Leguminosae. Spain.

ahmadii F. Petrak, Sydowia. Annales Mycologici, Horn, N.Ö. 8:167. 1954. On dry branches of *Capparis aphylla* Roth, Capparaceae. Pakistan.

ailanthi P.A. Karsten & P.A. Hariot, Journal de Botanique, Paris 3:206. 1889. On branches of *Ailanthus glandulosa* Desf., Simaroubaceae. France.

akagiensis E.A. Vainio, Botanical Magazine, Tokyo 35:79. 1921. On tree bark of unknown host, unknown family. Japan.

albopunctata (G.D. Westendorp) J.B. Ellis & B.M. Everhart, The North American Pyrenomycetes. A Contribution to Mycologic Botany, p. 375. 1892. ≡*Sphaeria albopunctata* G.D. Westendorp.

albopunctata (G.D. Westendorp) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:72. 1883. ≡*Sphaeria albopunctata* G.D. Westendorp, Bulletins de L'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique, Brussels, Series 2, 7:87–88. 1859. ≡*Heptameria* (*Leptosphaeria*) *albopunctata* (G.D. Westendorp) M.C. Cooke, Grevillea, London 17:32. 1889. ≡*Phaeosphaeria albopunctata* (G.D. Westendorp) R.A. Shoemaker, Canadian Journal of Botany, Ottawa 67:1566. 1989. On seeds of *Phragmites communis* Trin., Gramineae. Belgium.

albulae E. Müller, Sydowia. Annales Mycologici, Horn, N.Ö. 4(1–6):281. 1950. On dead stems of *Lonicera alpigena* L., Caprifoliaceae. Switzerland.

(*Leptosphaerella*) *alcides* P.A. Saccardo, Nuovo Giornale Botanico Italiano e Bolletino della Società Botanica Italiana, Firenze 8:176. 1876. On underside of leaves of *Populus alba* L., Salicaceae. Italy.

alcides P.A. Saccardo forma *quercina* R. Ciferri, Annales Mycologici, Berlin 20:51. 1922. On dry leaves of *Quercus robur* L., Fagaceae. Italy.

alexandrinis A. Negru, Mycopathologia et Mycologia Applicata, Den Haag 33:365–366. 1967. On leaves of *Cucumis sativus* L., Cucurbitaceae. Romania.

algarbiensis M.T. Lucas, Memórias da Sociedade Broteriana, Coimbra 21:34. 1970. On dead leaves of *Chamaerops humilus* L., Palmae. Portugal.

algida E. Rostrup, Meddelelser om Grønland, Kjøbenhavn 3:558. 1888. On leaves of *Catabrosa algida* Fr., Gramineae. Greenland.

alhagii I.P. Frolov, Novosti Sistematiki Nizshikh Rastenij, Novitates Systematicae Plantarum Non Vascularium 7:185–186. 1970. On dry branches of *Alhagi* sp., Leguminosae. U.S.S.R.

alhaginis I.P. Frolov *in* E.N. Koschkelova, I.P. Frolov, and Z. Dzhuraeva, Mikoflora Badkhyza, Karabilya i Yuzhnoĭ Chasti Murgabskogo Oazisa (Mikromitsety) [The Mycoflora of Badkhyz, Karabil and the Southern Part of the Murgab Oasis (Micromycetes)], p. 86. 1970. Nom. nud. Art. 32.1. ≡*Leptosphaeria alhagii* I.P. Frolov.

aliena H. Sydow, Annales Mycologici, Berlin 35:28–30. 1937. On leaves and culms of *Cladium articulatum* R. Br., Cyperaceae. Australia (New South Wales).

alliariae (L. Fuckel) J. Schröter *in* F.J. Cohn, Kryptogamen-Flora Von Schlesien. Im Namen Der Schlesischen Gesellschaft für

vaterländische Cultur herausgegeben von Prof. Dr. Ferdinand Cohn, Secretair der Botanischen Section, Breslau 3(2):364. 1894. ≡*Sphaeria aliriae* L. Fuckel, Symbolae Mycologicae, p. 135. 1870, sub. *Pleospora maculans*. On stems of *Alliaria officinalis* Andrz ex Bieb., Cruciferae. Poland.

alliariae (B. Auerswald) H. Rehm, Ascomyceten, Fascicle 14, No. 686. Anno 1882; Hedwigia, Dresden 22:56. 1883. ≡*Sphaeria alliariae* B. Auerswald *in* G.L. Rabenhorst, Fungi Europaei Exsiccati, Klotzschii Herbarii vivi Mycologici Continuatio, Edition 3, Century 3, No. 261. Anno 1860. On dry stems of *Sisymbrium alliaria* (L.) Scop., Cruciferae. Germany.

alliariae (B. Auerswald) G. Linhart, Fungi Hungarici Exsiccati [Magyarorszag Gombai], Century 2, No. 164. Anno 1883. Nom. illegit. Art. 64.1. ≡*Sphaeria alliariae* B. Auerswald *in* G.L. Rabenhorst, Fungi Europaei Exsiccati, Klotzschii Herbarii vivi Mycologici Continuatio, Edition 3, Century 3, No. 261. Anno 1860. On dry stems of *Brassica campestris* L., Cruciferae. Germany, Hungary.

allorgei A.L. Guyot, Revue de Mycologie, Paris 14:69. 1949. On dry stems of *Isatis tinctoria* L., Cruciferae. France.

almeidae M. de Sousa da Camara, Revista Agronómica, Lisbon, No. 1:11–12. 1928. [From reprint.] On leaves of *Cinnamomum zeylanicum* Blume, Lauraceae. Portugal.

almeidana M. de Sousa da Camara, Boletim de Agricultura, Lisboa 2(1):14. 1936. [Pagination on reprint, p. 21.] On branchlets of *Pinecenectria* sp., Agavaceae. Portugal.

aloes M.R. Sousa de Dias & M. de Sousa da Camara, Agronomia Lusitana, Sacavém 16:8. 1954. On leaves of *Aloe arborescens* Miller, Liliaceae. Portugal.

alopecuri N.N. Lavrov, Trudȳ Tomskogo Gosudarstvennogo Universiteta. Tomsk. Series Biologicheskii 110:76. 1951. On dead leaves of *Alopecurus borealis* Trin., Gramineae. U.S.S.R.

alpiniae A. Maublanc, Bulletin de la Société Mycologique de France, Paris 21:89. 1905. On leaves of *Alpinia speciosa* K. Sch., Zingiberaceae. Brazil.

altaica A. Nannizzi, Atti dell' Accademia dei Fisiocritici di Siena, Series 10, 3:961. 1928. On dried sheaths of leaves on *Polygonum bistorta* L., Polygonaceae. Yugoslavia.

alvariensis K. Starbäck, Bihang till K. Svenska Vetenskapsakademiens Handlingar, Stockholm, Series 3, 15(2):28. 1889. [Raised to specific rank in legend of Figure 4.] ≡*Leptosphaeria vagabunda* P.A. Saccardo subsp. *alvariensis* K. Starbäck.

ambiens H. Rehm, Philippine Journal of Science, Manila, Section C, 8:257. 1913. On dead branches of unknown host, unknown family. Philippines.

ammophilae (W.G. Lasch) V. Cesati & G. de Notaris, Commentario della Società Crittogamologica Italiana, Milan 1:236. 1863. ≡*Sphaeria ammophilae* W.G. Lasch *in* G.L. Rabenhorst, Klotzschii Herbarium Vivum Mycologicum Sistens Fungorum Per Totam Germaniam Cresentium Collectionem Perfectam, Dresden, Edition I, Century 14, No. 1340. Anno 1850; Flora, Jena und Regensburg 8:282. 1850; Botanische Zeitung, Berlin & Leipzig 8:439. 1850. ≡*Phaeosphaeria ammophilae* (W.G. Lasch) J. Kohlmeyer & E. Kohlmeyer, Icones Fungorum Maris Lief. 3, Table 55. 1965. ≡*Amarenomyces ammophilae* (W.G. Lasch) O. Eriksson, Nordic Journal of Botany, Copenhagen [Opera Botanica] 60:124. 1981. On leaves of *Ammophila arenaria* (L.) Link, *Elytrigia juncea* (L.) Nevski, Gramineae. Denmark, Finland, Germany, Netherlands, U.S.S.R.

ammophilae H. Rehm ex H. Rehm, Ascomyceten, Fascicle 14, No. 691. Anno 1882. Nom. nud. 32.1 [as (Lasch) Cesati & de Notaris]; Hedwigia, Dresden 22:57. 1883. Non *Leptosphaeria ammophilae* (W.G. Lasch) V. Cesati & G. de Notaris. On dry leaves of *Ammophila arenaria* (L.) Link, Gramineae. Germany.

ammophilae H. Rehm, falsely so cited *in* A.N. Berlese and P. Voglino, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo Additamenta Ad Volumina I–IV, p. 139. 1886; P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 9:790. 1891. ≡*Leptosphaeria ammophilae* (W.G. Lasch) V. Cesati & G. de Notaris.

ammothamni E.N. Koschkelova *in* E.N. Koschkelova, I.P. Frolov, and Z. Dzhuraeva, Mikoflora Badkhyza, Karabilya i Yuzhnoĭ Chasti Murgabskogo Oazisa (Mikromitsety) [The Mycoflora of Badkhyz, Karabil and the Southern Part of the Murgab Oasis (Micromycetes)], p. 87. 1970. Nom. nud. Art. 32.1. On dry branches of *Ammothamnus lehmannii* Bunge, Leguminosae. U.S.S.R. (Badkhyza, Karabilia).

ammothamni E.N. Koschkelova, Novosti Sistematiki Nizshikh Rastenij, Novitates Systematicae Plantarum Non Vascularium 7:176–177. 1970. On dry branches of *Ammothamnus lehmannii* Bunge, Leguminosae. U.S.S.R.

amorphae E. Mitroshina, Notulae Systematicae e Sectione Cryptogamica Instituti Botanici Nomine V.L. Komarov Academiae Scientia-

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L. octophragmia
Alpinia speciosa K. Sch.
L. alpiniae
Amaranthus sp.
L. eriophora
Ambrosia trifida L.
L. drechsleri
L. fulgida
Ambrosia sp.
L. doliolum
Ammophila arenaria (L.) Link
L. ammophilae
L. ammophilae forma *calamagrostidis-arenariae*
L. littoralis
L. perforans
Ammophila arundinacea Host
L. sabuletorum
Ammophila sp.
L. marram
Ammothamnus lehmannii Bunge
L. ammothamni
Amorpha fruticosa L.
L. amorphae
Ampelopsis heterophylla (Thunb.) Sieb. & Zucc.
L. vagabunda
Anacylus radiatus Loisel.
L. anacycli
Anaphalis sp.
L. doliolum
Anarrhinum bellidifolium (L.) Willd.
L. anarrhini
Andromeda tetragona L.
L. andromedae
L. hyperborea
Andromeda sp.
L. sublanosa
Andropogon glomeratus (Walt.) B.S.P.
L. subcompressa
Andropogon ischaemum L.
L. eustomoides
L. ischaemi
L. trimera
Andropogon muricatus Retz.
L. muricata
Andropogon saccharoides Swartz
L. puiggarii
Andropogon sp.
L. herpotrichoides
L. latebrosa
L. michotii
Androsace lactea L.
L. pachyasca
Anemone narcissiflora L.
L. raphidophora
Anemone sylvestris L.
L. anemones
Anemone virginiana L.
L. platypus
Angelica sylvestris L.
L. conoidea
L. conoidea forma *angelicae*
Angelica sp.
L. obesula
L. setosa
Anthemis tinctoria L.
L. dolioloides
L. tanaceti
Anthericum ramosum L.
L. antherici
Anthriscus sylvestris (L.) Hoffm.
L. dolioloides var. *inops*
Antirrhinum majus L.
L. thuemeniana
Antirrhinum siculum Miller
L. galiorum subsp. *antirrhini*
L. insulana
Apios fortunei Maxim.
L. apios
L. apios-fortunei
Apocynum sp.
L. doliolum
Aquilegia vulgaris L.
L. aquilegiae
Arabis alpina L.
L. arabidis
L. johansonii
Aralia sp.
L. doliolum
Araucaria imbricata Pav.
L. californica
Arbutus unedo L.
L. arbuti
Arctium sp.
L. doliolum
Areca sapida Soland. ex Hook. f.
L. arecae
Arenaria ciliata L.
L. auerswaldii
Armeria vulgaris Willd.
L. staritzii
Arrhenatherum avenaceum Beauv.
L. arrhenatheri
Arrhenatherum elatius (L.) Beauv. ex J. Presl. & C. Presl.
L. arrhenatheri
Artemisia absinthium L.
L. gloeospora
Artemisia annua L.
L. sydowiana
Artemisia austriaca Jacq.
L. compressa
Artemisia californica Less.
L. tumefaciens
Artemisia campestris L.
L. artemisiae
L. caespitosa
L. compressa
L. phaeospora
L. sydowiana
L. valesiaca
Artemisia camphorata Vill.
L. camphorata
Artemisia frigida Willd.
L. tetonensis
Artemisia herba-alba Asso
L. rothomagensis var. *artemisiae*
Artemisia tridentata Nutt.
L. lasioderma
Artemisia vulgaris L.
L. doliolum var. *subdisticha*
L. grammodes
L. hispanica
L. kalmusii
L. purpurea
L. uncinata
Artemisia sp.
L. cervispora
L. crustacea
L. owaniae
L. tumefaciens
Aruncus dioicus Fern.
L. umbrosa
Aruncus silvestris Kostel.
L. arunci
Arundinaria sp.
L. eumorpha
Arundo donax L.
L. donacina
L. recessa
L. rhodophaea
Asclepias syriaca L.
L. dearnessii
Asclepias sp.
L. doliolum
L. russellii
Asparagus officinalis L.
L. asparagi
L. asparagina
L. passeriniana
L. portoricensis
L. praeclara
L. punctoidea
L. socialis
Asparagus sp.
L. comatella
L. indica
Asperella japonica Hack.
L. asperellae

Asperula sp.
L. politis
Aspicilia calcarea (L.) Korb
L. crozalsii
Aspidistra elatior Blume
L. aspidistrae
Asplenium septentrionale (L.) Hoffm.
L. asplenii
Aster multiflorus Ait.
L. astericola
Aster sagittifolius Wedem. ex Willd.
L. asteris
Aster salignus Willd.
L. conoidea forma *asteris*
Aster sp.
L. doliolum
L. heliopsidis
Astrantia major L.
L. umbrosa
Atraphaxis muschketovii Krasnov
L. atraphaxidis
Atriplex hortensis L.
L. calvescens
Atriplex verrucifera Bieb.
L. atriplicis
Atriplex sp.
L. echinella
Avena sativa L.
L. korrae
Avena sp.
L. avenae
Avicennia marina (Forsk.) Vierh. var. *resiniferae* (Forst.) Bakh.
L. australiensis
Avicennia nitida Jacq.
L. avicenniae
Axonopsus compressus (Swartz) Beauv.
L. korrae
Azalea sp. (=*Rhododendron* sp.)
L. azaleae
Baccharis sp.
L. bicuspidata
Baeomyces rufus (Huds.) Rebent.
L. baeomycearia
L. neottizans
Baldingera arundinacea (L.) Dumort.
L. baldingerae
L. larseniana
Ballota acetabulosa (L.) Bentham
L. ballotae
Ballota nigra L.
L. slovacica
Bambusa sp.
L. amphiloga
L. bambusae
L. bambusicola
L. scabrispora
L. schneideriana
L. tigrisoides
L. weddellii
Baptisia sp.
L. comatella
Bardana sp.
L. bardanae
Barkhousia taraxacifolia (Thuill.) DC.
L. modesta var. *rubellula*
Berberis ilicifolia Forst.
L. berberidicola
Berberis petiolicola Wall.
L. punjabensis
Berberis vulgaris L.
L. berberidis forma *berberidis*
L. coniothyrium
Berberis sp.
L. inconspicua
Berteroa incana (L.) DC.
L. submaculans
Betula verrucosa Ehrh.
L. betulina
Betula sp.
L. betulina
L. waghorniana
Biebersteinia emodii Jaub. & Spach.
L. hollosiana
Blysmus compressus (L.) Panzer ex Link
L. petkovicensis var. *elymi*
Bocconia sp.
L. bocconiae
Bomarea caldasii (HBK) Asch. & Graebn.
L. bomareae
Borreria leucomela (L.) Mudd
L. leucomelaria
Brachypodium sylvaticum (Hudson) Beauv.
L. brachypodii
L. microscopica forma *brachypodii*
L. sylvatica
Brachypodium sp.
L. culmifraga var. *linearis*
Brassica campestris L.
L. alliariae
L. maculans
Brassica crispa Rafin.
L. salebrosa
Brassica napus L.
L. napi
Brassica oleifera Moench
L. maculans forma *denudata*
Brassica oleracea L.
L. cesatiana
Brassica rapa L.
L. nigrella
Brassica sp.
L. olericola
Braya sp.
L. norvegica
Briza media L.
L. brizae
L. media
Bromus asper Murray
L. culmifraga var. *bromicola*
Bromus inermis Leysser
L. avenaria
Broussonetia sp.
L. coniothyrium
Buddleja davidii Franch.
L. buddlejae
L. davidii
L. polini
Buphthalmum salicifolium L.
L. septemcellulata
Bupleurum falcatum L.
L. agnita var. *bupleuri*
Bupleurum petraeum L.
L. bupleuri
Bupleurum ranunculoides L.
L. ranunculoides
Buxus sempervirens L.
L. buxina
L. melanommoides
L. revocans
Cacalia hastata L.
L. doliolum var. *cacaliae*
Cacalia sp.
L. nitschkei
Calamogrostis epigejos (L.) Roth
L. culmorum forma *epigeii*
Calamagrostis montana Host
L. fuckelii
Calamagrostis sylvatica Host
L. quinta
Calamagrostis sp.
L. coccodes
L. graminum
L. intermedia
L. sparsa
Calligonum sp.
L. calligoni
Calluna vulgaris (L.) Hull
L. ericae
Calopogonium mucunoides Desv.
L. calopogonii
Camellia japonica L.
L. camelliae-japonicae
Camellia theifera Griff.
L. depressa
L. tornatospora
Camellia sp.
L. camelliae

Campanula zoysii Wulfen
L. pachyasca
L. plemeliana
Camphorosma monspeliaca L.
L. serbica
Camphorosma perennis Pall.
L. camphorosmae
Canna indica L.
L. cannae
Cannabis sativa L.
L. cannabina
L. woroninii
Capparis aphylla Roth
L. ahmadii
L. capparidicola
Capparis horrida L.
L. simillima
Capparis spinosa L.
L. capparidis
Cardamine sylvatica Link
L. trollii
Carduus carlinoides Gouan
L. carlinoides
Carduus defloratus L.
L. centaureae
Carduus nutans L.
L. carduina
Carduus scopulorum Greene
L. chrysanthemi
Carduus sp.
L. carduorum
Carex acutiformis Ehrh.
L. sparsa
Carex arenaria L.
L. cariciphila
Carex baldensis L.
L. kochiana
Carex firma Host
L. caricis-firmae
Carex folliculata L.
L. folliculata
Carex glauca Scop.
L. striolata var. *caricis-glaucae*
Carex gracillima Schwein.
L. folliculata var. *oxyspora*
Carex hirta L.
L. caricis
L. occulta
Carex hyperborea Drejer
L. macrotheca
Carex leporina L.
L. culmorum var. *paleicola*
Carex paludosa Good.
L. gigaspsora
L. puccinioides
L. rivalis
Carex panicea L.
L. caricina
Carex pendula Hudson
L. caricicola
L. caricis
Carex pulla Good.
L. caricinella
L. consobrina
Carex rigida Good.
L. macrotheca
Carex riparia Curtis
L. caricicola
Carex silvatica auct.
L. caricina
Carex vaginata Tausch
L. caricis
Carex vesicaria L.
L. paludosa
Carex vulpina L.
L. caricis-vulpinae
L. microscopica
L. microscopica var. *caricis-vulpinae*
Carex sp.
L. clara
L. cumana
L. epicarecta
L. hemicrypta
Carlina acaulis L.
L. anthophila
L. cynaracearum
Carlina vulgaris L.
L. doliolum
L. doliolum forma *carlinae-vulgaris*
Carpinus sp.
L. depressa
L. subsimilis
Carya sp.
L. cacuminispora
L. lejostega
L. leucoplaca
Cassia sp.
L. cassiaecola
Cassinia aculeata R. Br.
L. plagia
Castanea sp.
L. involucralis
Castilleja miniata Doug. ex Hook.
L. castillejae
L. concinna
Castilleja pallida (L.) Sprengel
L. castilleiae
Catabrosa algida Fr.
L. algida
Ceanothus sp.
L. ceanothi
Cecropia peltata L.
L. cecropiae
Centaurea jacea L.
L. jaceae
Centaurea scabiosa L.
L. centaureae
Centranthus sp.
L. galiicola var. *brachyspora*
Cephalaria uralensis (Murray) Roemer & Schultes
L. cephalariai-uralensis
L. taurica
Cerastium biebersteinii DC.
L. biebersteinii
Cercocarpus ledifolius Nutt. ex Torr. & Gray
L. cercocarpi
Cereus peruvianus (L.) Miller
L. cerei-peruviani
Chaerophyllum aureum L.
L. agnita var. *major*
Chamaerops excelsior Boj
L. spatharum
Chamaerops humilis L.
L. algarbiensis
L. chamaeropis
L. debeauxii
L. magnusiana
Chamaerops sp.
L. pruni forma *plurivora*
Cheiranthus annuus L.
L. impressa
Chelidonium majus L.
L. chelidonii
Chenopodium album L.
L. calvescens
L. chenopodii-albi
L. eutypoides
L. inculta
L. nigricans
Chenopodium anthelminticum Bert. ex Steud.
L. anthelmintica
Chenopodium sp.
L. eriophora
Chimonanthus sp.
L. coniothyrium
Chondrilla juncea L.
L. bella
L. eburnea
L. mirabilis
L. trichostoma
Chondrus crispus J. Stackhouse
L. chondri
L. danica
L. marina
Chrysanthemum corymbosum L.
L. agnita var. *chrysanthemi*
Chrysanthemum leucanthemum L.
L. tanaceti
Chrysanthemum vulgare (L.) Bernh.
L. dolioloides
L. tanaceti
Chrysothamnus graveolens (Nutt.) Greene
L. arthrophyma

Chusquea serrulata Pilger
L. chusqueae
L. saginata
Chusquea sp.
L. consociata
L. stellata
Cicclidotus fontinaloides (Hedw.) P. Beauv.
L. cinclidoti
Cinnamomum camphora T. Nees ex Eberm.
L. cinnamomi
Cinnamomum zeylanicum Blume
L. almeidae
Cirsium altissimum (L.) Spreng.
L. compressa
Cirsium arvense (L.) Scop.
L. cirsii-arvensis
Cirsium lanceolatum (L.) Scop.
L. corynispora
Cirsium muticum Michx.
L. mesoedema
Cirsium palustre (L.) Scop.
L. galiorum forma *cirsiorum*
Cirsium sp.
L. dolioloides var. *cirsii*
L. doliolum
Cistus albidus L.
L. cisti
Cistus ladanifer L.
L. cistina
Cistus monspeliensis L.
L. cisticola
Citrus aurantium L.
L. bondari
L. papulosa
Citrus grandis Osb.
L. bondari
Citrus limonia Osb.
L. bondari
Citrus limonum Risso
L. vagabunda forma *citri-limonii*
Citrus medica L.
L. bondari
Citrus sinensis Osb.
L. bondari
Citrus sp.
L. bondari
L. citricola
Cladium articulatum R. Br.
L. aliena
Cladium mariscus (L.) Pohl
L. cladii
L. crucheti
Clematis recta L.
L. aucta
Clematis vitalba L.
L. agminalis
L. agminalis forma *minor*
L. grignonnensis
L. haematites
L. incruenta
L. nectrioides
L. pleosporoides
L. pyrenopezizoides
L. rimalis
L. vagabunda
L. vitalbae
L. vitalbae var. *sarmenticola*
Clerodendrum foetidi Bunge
L. clerodendri
Coccothrinax argentata (Jacq.) Bailey
L. coccothrinacis
Cocos romanzoffiana Cham.
L. cocoes
L. molleriana
Coffea arabica L.
L. coffeigena
Coffea canephora Pierre ex Froehn.
L. canephorae
L. coffeigena var. *longirostrata*
Coffea excelsa Cheval.
L. centrafricana
L. excelsa
L. lobayensis
L. longispora
Coffea robusta L. Linden
L. africana
L. cylindrospora
L. gigaspora
L. macrorostra
L. oubanguiensis
L. tetraspora
Coffea sp.
L. coffaeicida
L. pusilla
L. tonduzi
Coix lacryma-jobi L. var. *susutama* Honda
L. coicis
Coleosanthus reniformis (Gray) Rydb.
L. coleosanthi
Collinsonia canadensis L.
L. collinsoniae
Collomia squarrosa Nutt.
L. collumiae
Colocasia antiquorum Schott
L. colocasiae
Conium maculatum L.
L. conii
L. coniigena
L. rubicunda
Convallaria majalis L.
L. smarodsii
Convallaria multiflora L.
L. convallariae
Convallaria polygonatum L.
L. bellynckii
Cora pavonia (Swartz) Fries
L. corae
Corallorrhiza multiflora Nutt.
L. corallorhizae
Cordyline dracaenoides Kunth
L. cordylines
Cornus alba L.
L. limitata
Cornus florida L.
L. olivaespora
Cornus sanguinea L.
L. corticola
L. fiedlaeri
L. limitata
L. platycarpa
L. vagabunda
Cornus stolonifera Michx.
L. rugosa
Cornus sp.
L. mamillana
Coronilla coronata L.
L. dumetorum var. *coronillae*
Coronilla emerus L.
L. riofrioi
Coronilla sp. [as *C. comata* L.]
L. coronillae
Corvus cornix [Animalia]
L. corvina
Corylus avellana L.
L. avellanae
L. vagabunda
Corylus sp.
L. leucoplaca
Cosmos sulphureus Cav.
L. cosmicola
Coumarouna punctata S.F. Blake
L. coumarounae
Cousinia multiloba DC.
L. shahvarica
Crataegus monogyna Jacq.
L. pomona forma *transilvanica*
Crataegus oxyacantha L.
L. saccardiana
Crepis sibirica L.
L. sibirica
Crepis vesicaria L. subsp. *haenseleri* (Boiss. ex DC.) P.D. Sell
L. rubellula
Crithmum maritimum L.
L. helminthospora forma *crithimi-maritimi*
L. rhopalispora
Cucumis sativus L.
L. alexandrinis

Cucurbita pepo L.
L. cucurbitae
Cycas revoluta Thunb.
L. cycadis
L. irrepta
Cynanchum sp.
L. modesta var. *cibostii*
L. scotophila
Cynodon dactylon (L.) Pers.
L. cynodontis-dactyli
L. korrae
L. narmari
L. rhizomatum
Cynodon transvaalensis Burtt-Davy
L. narmari
Cynodon sp.
L. pontiformis
Cynoglossum officinale L.
L. cynoglossi
L. vindobonensis
Cynosurus cristatus L.
L. cynosuri
Cyperus flavescens L.
L. cyperi
L. cypericola
Cyperus monti L.
L. cyperina
Cyperus papyrus L.
L. papyri
Cyperus schoenoides Griseb.
L. ceballosi
Cytisus alpinus Miller
L. corrugans
Cytisus laburnum L.
L. lucina
Dactylis glomerata L.
L. caricis
L. culmicola var. *nigrans*
L. dactylina
L. nigrans
L. recutita
Danthonia frigida Vickery
L. gaubae
Daphne gnidium L.
L. daphnes
L. vagabunda forma *daphnes*
Daphniphyllum macropodium Miq.
L. daphniphylli
Dasylirion junceum Zucc.
L. dasylirii
Dasystoma sp.
L. doliolum
Datura stramonium L.
L. caballeroi
Daucus carota L.
L. longipedicellata
L. rostrupii
Daucus sp.
L. comatella
L. modesta forma *dauci*
Daviesia latifolia R. Br.
L. daviesiae
Desmodium sp.
L. dissiliens
L. distributa
Desmoncus sp.
L. desmonci
Deutzia scabra Thunb.
L. dichroa
Dianella revoluta R. Br.
L. williamsii
Dianthus atrorubens All.
L. leptospora
Dianthus caryophyllus L.
L. dianthi
Dianthus prolifer L.
L. proliferae?
Dianthus superbus L.
L. dianthi
Dianthus sp.
L. dianthi
Dichosciadium ranunculaceum (F. v. Mueller) Domin
L. dichosciadii
Didymella vincetoxici (de Not.) Sacc.
L. didymellae-vincetoxici
Digitalis lutea L.
L. modesta forma *digitalis-luteae*
Digitalis purpurea L.
L. valdiviensis
Digitalis sp.
L. digitalis
Dipsacus sylvestris Hudson
L. bractearum var. *bractearum*
L. carpophila
L. modesta forma *sylvestris*
Dodonaea viscosa (L.) Jacq.
L. dodonaeae
Dorycnium suffruticosum Vill.
L. cucurbitarioides
Draba alpina L.
L. drabae
Dracaena draco (L.) L.
L. convallariae
L. convallariae forma *dracaenae*
L. dracaenae
L. draconis
Dryas octopetala L.
L. dryadis
L. rostrupii
Drypis spinosa L.
L. rehmiana
Dulcamara sp.
L. vagabunda
Dupontia fisheri R. Br.
L. insignis
L. vagans
L. vagans forma *scirpi*
Dupontia psilosantha (Rupr.) Griseb.
L. insignis
Echium vulgare L.
L. cesatiana
L. echiella
L. echii
Eichhornia crassipes (C.F.P. Mart.) Solms-Laub.
L. eichhorniae
Elaeis guineensis Jacq.
L. elaeidicola
L. elaeidis
Eleocharis sp.
L. norfolcia
Elymus arenarius L.
L. arenaria
L. elymi
L. larseniana
L. quinta
Elymus? barbatus F. Kurtz.
L. lagenoides
Elymus glaucus Buckley
L. elongata
Elymus sp.
L. elymi
Elyna spicata Schrader
L. sparsa var. *elynae*
Elytrigia juncea (L.) Nevski
L. ammophilae
Empetrum nigrum L.
L. empetri
Endiusa hirsuta Alef.
L. endiusae
Ephedra distachya L.
L. ephedrae
Epichloe typhina (Pers.:Fr.) Tul.
L. associata
Epilobium angustifolium L.
L. cylindrospora
Epilobium dodonaei Vill.
L. cadubriae
Epilobium fleischeri Hochst.
L. epilobii
L. multiseptata forma *alpina*
Epilobium hirsutum L.
L. tritorulosa
Epilobium montanum L.
L. epilobii
Epilobium trigonum Schrank
L. epilobii
Equisetum arvense L.
L. arvensis
Equisetum hyemale L.
L. berlesei
L. hiemalis

Equisetum limosum L.
L. limosa
Equisetum variegatum Schleicher ex Weber & Mohr
L. equiseti
L. equiseticola
Equisetum sp. [as *E. pallidum*]
L. larvalis
Eranthemum sp.
L. eranthemi
Eremochloa ophiuroides (Munro) Hack.
L. korrae
Erianthus alopecuroides (L.) Ell.
L. orthogramma
Erica carnea L.
L. subtecta
Erigeron canadensis L.
L. agnita var. *erigerontis*
L. canadensis
L. congesta
Erigeron viscidus Rydb.
L. erigerontis
Erigeron sp.
L. doliolum
L. plurisepta
Eriobotrya japonica (Thunb.) Lindley
L. eriobotryae
L. miyakeana
L. puttemansii
Eryngium agavifolilum Griseb.
L. vinosa
Eryngium campestre L.
L. eryngii
L. nigrella
L. woodrow-wilsonii
Erysimum cheiranthoides L.
L. submaculans
Erysimum diffusum Ehrh.
L. acutispora
Erysimum erysimoides (L.) Fritsch ex Janchen
L. acutispora
Erysimum hieracifolium L.
L. fusispora forma *erysimi*
Erythrina crista-galli L.
L. aerea
Erythrina sp.
L. erythrinae
Espeletia neriifolia Sch. Bip. ex Wedd.
L. jahnii
Espeletia sp. (*?E. schultzii* Wedd.)
L. espeletiae
Eucalyptus globulus Labill.
L. molleriana
Euonymus europaeus L.
L. castagnei
L. constricta
Euonymus sp.
L. californica
Eupatorium cannabinum L.
L. agnita var. *ambigua*
L. cerastii
Eupatorium capillifolium (Lam.) Small
L. clavispora
Eupatorium coronopifolium Willd.
L. mesoedema
Eupatorium maculatum L.
L. jacksonii
Eupatorium purpureum L.
L. jacksonii
Eupatorium saucechicoense Hieron.
L. preandina
Eupatorium sp.
L. doliolum
Euphorbia cyparissias L.
L. euphorbiae
Euphorbia dendroides L.
L. sacculus
Euphorbia esula L.
L. euphorbiae forma *esulae*
Euphorbia osyridea Boiss.
L. euphorbiicolla
Euphorbia oxyroidea [authority unknown]
L. depressa
Euphorbia pilosa L.
L. euphorbiaecola
Euphorbia sibthorpii Boiss.
L. sibtorpii
Euphorbia wulfenii Hoppe ex Koch
L. bresadolaeana
Euphorbia sp.
L. tolgorensis
Euphrasia lutea L.
L. coniformis
Eustephia sp.
L. australis
Fagus sylvatica L.
L. valdobbiae
Fagus sp.
L. faginea
L. seminuda
Farsetia incana (L.) R. Br.
L. conferta
Feijoa sp. [as *F. feijoicola*]
L. feijoae
Ferula badra-kema K. Pol.
L. ferulicola
Festuca arenaria Osbeck
L. arenaria
Festuca arundinacea Schreber
L. sabuletorum
Festuca kerguelensis Hook. f.
L. kerguelensis
Festuca sp.
L. crastophila
L. eustomella
L. stromatoidea
L. taminensis
Ficus elastica Roxb.
L. fici-elasticae
Filipendula ulmaria Maxim.
L. obesula
L. rustica
Flotovia excelsa DC.
L. flotoviae
Foeniculum vulgare Miller
L. foeniculacea
L. foeniculi
Foeniculum sp.
L. doliolum
L. doliolum var. *pinquicula*
Francoa sonchifoliae Cav.
L. francoae
Frasera speciosa Dougl. ex Griseb.
L. fraserae
Frasera? sp.
L. harknessianna
Fraxinus americana L.
L. fraxini
Fraxinus sp.
L. controversa
L. leucoplaca
Fungi
L. associata
L. caucana
L. cryptica
L. didymellae-vincetoxici
L. fungicola
L. geasteris
L. phyllachoricola
L. phyllachorivora
L. platychorae
L. stereicola
L. tungurahuensis
Furcraea bedinghausii C. Koch
L. rusci forma *fourcroyae*
Furcraea longaeva Karw. & Zucc.
L. infernalis
Furcraea sp.
L. translucens
Galeobdolon luteum Hudson
L. galeobdolonis
Galeopsis speciosa Miller
L. galeopsidicola
Galium aparine L.
L. aparines
L. scitula
Galium boreale L.
L. dumetorum var. *galii-borealis*
Galium mollugo L.
L. galiicola

L. molluginis
L. plectrospora
Galium sylvaticum L.
L. galii-silvatici
Galium sp.
L. galii
L. galiorum
Gaultheria shallon Pursh
L. gaultheriae
Geaster pseudolimbatus Hollós
L. geasteris
Genista anglica L.
L. genistae
Genista ferox Poir.
L. phiala
Genista tinctoria L.
L. fusispora
L. genistae var. *microspora*
Gentiana asclepiadea L.
L. umbrosa
Gentiana lutea L.
L. galiorum forma *gentianae*
L. salebrosa
L. sapeyensis
Geranium richardsonii Fisch. & Trautv.
L. modestula
Geranium sp.
L. subcaespitosa
Gerardia sp.
L. doliolum
Ginkgo biloba L.
L. ginkgo
Glyceria aquatica (L.) Wahlenb.
L. microscopica forma *glyceriae*
L. recutita
Glyceria fluitans (L.) R. Br.
L. glyceriae
Glyceria plicata (Fries) Fries
L. glyceriae-plicatae
Glyceria spectabilis Mert. & Koch
L. culmorum var. *flavobrunnea*
Gnaphalium sp.
L. galiorum var. *gnaphaliana*
L. gnaphalii
Gossypium sp.
L. gossypii
Grindelia? sp.
L. nigricans var. *grindeliae*
Guazuma sp.
L. guazumae
Gymnadenia conopsea (L.) R. Br.
L. orchidearum
Gynerium argenteum Nees
L. gynerii
L. subiculifera?
Gypsophila paniculata L.
L. gypsophilae
Haloxylon aphyllum (Minkw.) Iljin
L. haloxyli
Hamemelis virginiana L.
L. hamamelidis
Hardenbergia violacea (Schneev.) Stearn
L. hardenbergiae
Hedera helix L.
L. hederae
L. hedericola
L. helicicola
L. papulosa
Hedysarum obscurum L.
L. chochrjakovii
Heleocharis palustris (L.) Roem. & Schult.
L. sowerbyi
Helianthemum sp.
L. helianthemi
Helianthus annuus L.
L. drechsleri
L. helianthi
L. lindquistii
Helianthus giganteus L.
L. helianthi
Helianthus grosserratus Martens
L. drechsleri
Helianthus sp.
L. consessa
L. doliolum
L. heliopsidis
Heliopsis sp.
L. drechsleri
L. heliopsidis
Helleborus foetidus L.
L. lathonia
Helleborus viridis L.
L. lathonia var. *hellebori-foetidi*
Helonias bullata L.
L. heloniaefolia
Hemerocallis sp.
L. hemerocallidis
Heracleum lanatum Michx.
L. simmonsii
Heracleum palmatum Baumg.
L. doliolum var. *dissimilis*
Heracleum sphondylium L.
L. massarioides
Heracleum sp.
L. doliolum
Hermodactylus tuberosus (L.) Miller
L. hermodactyli
Hesperis dinarica G. Beck
L. hesperidicola
Hesperis sp.
L. galiicola var. *brachyspora*
Hevea brasiliensis Müll. Arg.
L. heveae
Hicoria sp.
L. exocarpogena
Hieracium murorum L.
L. brauni
Hierochloë alpina (Willd.) Roemer & Schultes
L. hierochloae
Hierochloë ëantarctica R. Br.
L. fuegiana
Hippophaë rhamnoides L.
L. fuscella var. *hippophaes*
L. fuscella var. *sydowiana*
L. hippophaes
Homo sapiens
L. senegalensis
L. tompkinsii
Hordeum arenarium Ascherson
L. arenaria
Hordeum distichon L.
L. recutita
Hordeum turkestanicum Nevski
L. hordei
Hordeum vulgare L.
L. narmari
L. nodorum form sp. *hordei*
Humulus lupulus L.
L. dumetorum
Hura crepitans L.
L. hurae
Hydrangea arborescens L.
L. hydrangeae
Hydrocotyle asiatica L.
L. nesodes
Hyparrhenia sp.
L. hyparrheniae
Hypericum alpestris Stev. ex Ledeb.
L. hypericola
Hypericum calycinum L.
L. vagabunda
Hypericum perforatum L.
L. cesatiana
L. dematium
L. hyperici
L. lankeana
L. ocellata
Ilex paraguariensis A. St. Hil.
L. paraguariensis
L. yerbae
Inula crithmoides L.
L. helminthospora
L. rhopalispora
Inula salicina L.
L. derasa var. *franconica*
L. franconica

Ipomoea batatas (L.) Lam.
L. bataticola
L. ferruginea
Iris arenaria Waldst. & Kit.
L. iridis
Iris foetidissima L.
L. iridicola
L. vectis
L. xiphii
Iris germanica L.
L. heterospora
L. parvula var. *iridis-germanicae*
Iris pseudacorus L.
L. iridigena
L. larseniana
L. longispora
L. microthyrioides
L. parvula
Isatis tinctoria L.
L. allorgei
Jambosa malaccensis DC.
L. eustomoides var. *punctata*
Jasminum fruticans L.
L. emiliana
Jubaea spectabilis Humb., Bonpl., & Kunth
L. briosiana
L. jubaeae
Juglans regia L.
L. petiolaris
Juglans sp.
L. leucoplaca
Juncus acutiflorus Ehrh. ex Hoffm.
L. juncorum
Juncus acutus L.
L. junci-acuti
Juncus articulatus L.
L. therophila
Juncus biglumis L.
L. junciseda
Juncus drummondii E. Mey.
L. solheimii
Juncus effusus L.
L. defodiens
L. hydrophila
L. junci
L. juncina
L. petkovicensis
L. pseudo-diaporthe
L. riparia
L. viridella
Juncus filiformis L.
L. sepalorum
Juncus glaucus Sibth.
L. junci
L. junci-glauci
L. subriparia
L. vitensis
Juncus hostii Tausch
L. juncicola
Juncus lampocarpus Ehrh. ex Hoffm.
L. lamprocarpi
L. monilispora
Juncus maritimus Lam.
L. maritima
L. neomaritima
Juncus roemerianus Scheele
L. neomaritima
Juncus trifidus L.
L. juncicola
L. sepalorum
Juncus sp.
L. michotii
L. norfolcia
L. variabilis
Juniperus communis L.
L. juniperi
Juniperus nana Willd.
L. juniperina
L. saprophila
Kalmia angustifolia L.
L. kalmiae
Kerria japonica (L.) DC.
L. vagabunda
Kerria sp.
L. coniothyrium
L. vagabunda var. *divergens*
Kigelia pinnata DC.
L. dryadea subsp. *lussoniensis*
Knautia arvensis (L.) Coulter
L. phyteumatis
Koeleria albescens DC.
L. clavata
Koeleria cristata (L.) Pers.
L. herpotrichoides
Koeleria gracilis Pers.
L. clavata
Koerberiella wimmeriana (Koerber) B. Stein
L. koerberi
Lactuca muralis (L.) Gaertner
L. quadriseptata
Lactuca sp.
L. doliolum
Lagotis minor (Willd.) Standley
L. holmii
Lamium album L.
L. parietariae forma *lamii*
Lantana camara L.
L. isocellula
L. rajasthanensis
Lappa sp.
L. eriophora
L. galiicola var. *brachyspora*
L. modesta forma *lappae*
Lapsana communis L.
L. galiorum var. *lapsanae*
Laserpitium angustifolium Georgi
L. oreophiloides
Laserpitium halleri Crantz
L. ladina
Laserpitium latifolium L.
L. ettalensis
Laserpitium siler L.
L. cornuta
L. sileris
Laserpitium sp.
L. spectabilis
Lathyrus latifolius L.
L. lathyrina
L. niessleana
Lathyrus niger (L.) Bernh.
L. dolioloides var. *lathyri*
Lathyrus sylvestris L.
L. lathyri
L. multiseptata
Laurus nobilis L.
L. lauri
L. nobilis
L. paoluccii
Laurus sp.
L. coniothyrium var. *foliicola*
Lavandula stoechas L.
L. lavandulae
Lavandula vera DC.
L. salviae forma *minor*
Lavandula sp.
L. cavanillesii
Lecanora frustulosa (Dicks.) Ach.
L. steinii
Lecidea excentrica Roehling
L. advenula
Lecidea vernalis (L.) Ach.
L. consocians
Leersia oryzoides (L.) Swartz
L. leersiae
L. leersiana
Leleba sp. [as *L. simplex*]
L. lelebae
Lemanea pluviale C. Aq.
L. fluviatilis
L. lemaneae
Leonurus cardiaca L.
L. doliolum var. *leonuri*
Lepidium campestre (L.) R. Br.
L. ogilviensis forma *lepidii*
Lepidium virginicum L.
L. virginica
Leptorhaphis leptogiophila Minks ex Wint.
L. leptogiophila
Lepus europaeus
L. fimiseda
Lespedeza bicolor Turcz.
L. lespedezae

Lespedeza capitata Michx.
L. microspora
Liatris scariosa (L.) Willd.
L. trimerioides
Libanotis montana Crantz
L. foliicola
L. libanotis
Libanotis sp.
L. longchampsi
Lichenes
L. advenula
L. apocalypta
L. arnoldii
L. baeomycearia
L. caninae
L. clarkii
L. consocians
L. corae
L. crozalsii
L. galligena
L. geographicola
L. inarensis
L. koerberi
L. leptogiophila
L. leucomelaria
L. lichenicola
L. maheui
L. mamillula
L. neottizans
L. oligospora
L. parmeliarum
L. peltigerarum
L. peltigerea
L. polaris
L. pycnostigma
L. ramalinae
L. rivana
L. rivana forma *solorinae*
L. sphyridiana
L. steinii
L. stereocaulorum
L. tartarina
L. umbilicariae
L. usneae
Lilium martagon L.
L. martagoni
Lilium superbum L.
L. lilii
Lilium sp.
L. lilicola
Linum tenuifolium L.
L. hrubyana
Lippia (Aloysia) citriodora Kunth
L. octophragmia var. *major*
Lippia seriphioides A. Gray
L. basalduai
Liriodendron tulipifera L.
L. halima
Liriodendron sp.
L. stictoides

Lobelia excelsa Lesch.
L. lobeliae
Lobelia tupa L.
L. tupae
Lolium perenne L.
L. eustomoides
L. lolii
Lomatia obliqua R. Br.
L. chilensis
Lonicera alpigena L.
L. albulae
Lonicera canadensis Bartr.
L. lonicerae
Lonicera caprifolium L.
L. caprifolii
L. corticola
Lonicera periclymenum L.
L. periclymeni
Lonicera tatarica L.
L. frondis
L. periclymeni var. *tatarica*
L. surculorum
Lonicera xylosteum L.
L. lonicerae
Lonicera sp.
L. aulica
L. lonicerae
Lophanthus sp.
L. lophanthi
Lunaria rediviva L.
L. lunariae
Lupinus sp.
L. barriae
L. byssincola
L. foeniculacea subsp. *lupina*
L. frigida
L. lupini
L. lupinicola
Lupinis latifolius J.G. Agardh
L. wehmeyeri
Lupinus obtusilobus
L. castrensis
Lupinus rubricaulis Greene
L. wehmeyeri
Lupunus albicaulis var. *shastensis*
L. shastensis
Luzula albida (Hoffm.) DC.
L. culmorum forma *hungarica*
L. epicalamia var. *pleosporoides*
L. juncina forma *macrospora*
Luzula lutea (All.) DC.
L. epicalamia
L. microscopica var. *alpina*
Luzula maxima (Reichard) DC.
L. luzulae

Luzula nemorosa (Pollich) E.H.F. Meyer
L. epicalamia
L. petrakii
Luzula sylvatica (Hudson) Gaudin
L. caricis
L. epicalamia
Lycium vulgare Dunal.
L. lyciophila
Lycopodium annotinum L.
L. campisilii
L. crepini
L. lycopodina
L. marcyensis
Lycopodium clavatum L.
L. lycopodiicola
Lycopodium selago L.
L. marcyensis
Lycopodium selago L. var. *appressum* Desv.
L. arctalaskana
Lycopus europaeus L.
L. cesatiana
Lygeum spartum L.
L. spartii
Lythrum alatum Pursh
L. lythri
Lythrum salicaria L.
L. salicaria
Maclura aurantiaca Nutt.
L. maclurae
Magnolia grandiflora L.
L. magnoliae
Magnolia yulan Desf.
L. yulan
Malus domestica Borkh.
L. mandshurica
L. pomona
L. ternata
Malus sp.
L. concentrica
Manihot utilissima Pohl
L. petri
Maranta arundinacea L.
L. marantae
Marattia sp.
L. caffra
Marrubium vulgare L.
L. dumetorum var. *marrubii*
Matisia paraensis Hub.
L. matisiae
Medicago falcata L.
L. blumeri
Medicago sativa L.
L. circinans
L. medicaginicola
L. medicaginis
L. pratensis

Medicago sp.
L. medicaginis
L. medicaginum
Melampyrum pratense L.
L. suffulta
Melandrium apetalum (L.) Fenzl
L. vanhoeffeniana
Melandrium triflorum J. Vahl. ex Liebm.
L. vahlii
Melica altissima L.
L. culmicola forma *melicae*
L. fuscidula
Melica inaequiglumis Boiss.
L. melicae
Melica magnolii Gren. & Godron
L. fuscidula forma *magnolii*
Melica uniflora Retz.
L. melicae
Melilotus alba Medicus
L. dumetorum forma *meliloti*
L. meliloti
Melilotus sp.
L. viridella
Menispermum canadense L.
L. coniothyrium
Mentha piperita L.
L. substerilis
Mentha sylvestris L.
L. menthae
L. zahlbruckneri
Mertensia sp.
L. mertensiae
Mesogloia leveillei (J. Ag.) Mengh.
L. mirandae
Metasequoia glyptostroboides Hu & Cheng
L. metasequoiae
Mikania sp.
L. agnita var. *acheniarum*
L. mikaniae
Milium effusum L.
L. linearis
Minuartia sedoides (L.) Hiern.
L. dennisiana
Monotes dasyanthus Gilg.
L. baumii
Moriera sp.
L. morierae
Morus alba L.
L. fallax
L. massariella var. *disticha*
Morus sp.
L. japonica
Muehlenbeckia platyclados Meissn.
L. muehlenbeckiae
Muehlenbergia filiformis Rydb.
L. georgius-fischeri
Muehlenbergia racemosa (Michx.) Britton, Stern, & Pogg.
L. muehlenbergiae
Musa cavendishii Lamb. ex Paxton
L. musae
L. musigena
Musa sp.
L. musarum
L. taichungensis
Muscari comosum (L.) Miller
L. muscari
Musci
L. bryophila
L. cinclidoti
L. heufleri
L. polytrichina
Myrica gale L.
L. myricae
Myrrhis odorata (L.) Scop.
L. ogilviensis forma *myrrhis-odorata*
Myrtus communis L.
L. myrti
L. myrticola
Nandina domestica Thunb.
L. nandinae
Nardus stricta L.
L. nardi
L. pachytheca
Obione portulacoides (L.) Moq.
L. obiones var. *evolutior*
Obione sp.
L. obiones
Ochrolechia tartarea (L.) Massal
L. tartarina?
Ocimum sanctum L.
L. ocimicola
Oenothera biennis L.
L. capsularum
L. ellisiana
Oenothera longiflora L.
L. argentina
Onagra strigosa Rydb.
L. onagrae
Onobrychis sativa Link
L. onobrychidicola
L. onobrychidis
Ophiopogon japonicus Ker-Gawl.
L. ophiopogonis
Opuntia ficus-indica (L.) Miller
L. sicula
Opuntia lindheimeri Engelm.
L. opuntiae
Ornithogalum pyrenaicum L.
L. ornithogali
Orthrosanthus chimboracensis Baker
L. orthrosanthi
Oryza sativa L.
L. cattanei
L. inecola
L. iwamotoi
L. korrae
L. narmari
L. oryzae
L. oryzicola
L. oryzina
L. salvinii
Oryzopsis miliacea (L.) Bentham & Hooker ex Ascherson & Graebner
L. papillosa
Oxalis stricta L.
L. aglaja
Oxyria digyna (L.) Hill
L. oxyriae
Paeonia moutan Sims.
L. moutan
Palm
L. trochus
Pandanus odoratissimus Nor.
L. pandanicola
Pandanus utilis Bory
L. pandani
Panicum crus-galli L.
L. occidentalis
Panicum grumosum Nees
L. anthostomella
L. melanommoides
L. subsuperficialis
Panicum palmaefolium Koen.
L. panici
Papaver radicatum Rottb.
L. papaveris
Parietaria officinalis L.
L. muralis
L. parietariae
Parmelia saxatilis (L.) Arch.
L. parmeliarum
Parmelia sp. [as *P. atrata* Zahlbr.]
L. galligena
Paspalum giganteum Baldw. ex Vasey
L. proteispora
Pastinaca sativa L.
L. clivensis
Pastinaca sp.
L. doliolum
L. setosa
Pedicularis brachyodonta Schlosser & Vuk. var. *fallacis* (Beck) Hayek
L. malyi
Pedicularis bracteosa Benth. ex Hook.
L. jacksonensis

Pedicularis debilis Franch. ex Maxim.
L. doliolum var. *angustispora*
Pelargonium capitatum (L.) L'Her.
L. elaoudi
Pelargonium sp.
L. pelargonii
Peltigera aphthosa (L.) Willd. forma *complicata* Th. Fries
L. peltigerarum
Peltigera canina (L.) Willd.
L. caninae
L. mamillula
L. rivana
Peltigera malacea (Ach.) Funck.
L. arnoldii
Peltigera cf. *rufescens* (Weis.) Humb.
L. clarkii
Peltigera sp.
L. peltigerea
Pennisetum clandestinum Hochst. ex Chiov.
L. narmari
Pennisetum purpureum Schum.
L. penniseti
L. penniseticola
Penstemon confertus Dougl. ex Lindl.
L. lethalis
Periclymenum sp.
L. vagabunda forma *lonicerae*
Persea americana P. Mill.
L. gratissima
L. gratissima var. *longispora*
Persea lingue Nees
L. lingue
Petasites sp.
L. vagabunda var. *caulium*
Petroselinum hortense auct.
L. melanommoides
Peucedanum cervaria (L.) Lapeyr.
L. penicillus
Peucedanum longifolium Waldst. & Kit.
L. doliolum forma *syndoliola*
Phaca alpina L.
L. phacae
Phalaris arundinacea L.
L. fuckelii forma *filamentifera*
Phaseolus vulgaris L.
L. phaseoli
L. phaseolorum
Phleum arenarium L.
L. arenaria
Phleum boehmeri Wibel.
L. rousseliana
L. sequana
Phleum pratense L.
L. culmifida
Phlox decussata Lyon
L. phlogis
Phoenix canariensis Hort. ex Chabaud
L. batumensis
Phoenix dactylifera L.
L. phoenicis
L. pinnarum
L. pinnarum var. *rachidis*
Phoradendron townsendii Trel.
L. phoradendri
Phormium sp.
L. phormicola
L. phormii
L. roumegueri
Phragmites communis Trin.
L. albo-punctata
L. arundinacea
L. arundinacea var. *godini*
L. clavicarpa
L. culmicola var. *hispalensis*
L. culmorum forma *phragmitis*
L. elaeospora
L. graminis
L. larseniana
L. nigrans forma *arundinis*
L. perpusilla
L. phragmiticola
L. subalpina
L. typharum subsp. *phragmatina*
L. vaginae
Phragmites sp.
L. arundinacea
L. culmicola var. *rhizomatum*
L. cumulata
L. mosana
Phyllachora disseminata Syd.
L. phyllachoricola
Phyllachora graminis (Pers.:Fr.) Fuckel
L. phyllachorivora
Phyllachora tunguraluensis Petrak
L. tunguraluensis
Phyllachora sp.
L. caucana
L. cryptica
Phyllostachys bambuoides Siebold & Zucc.
L. bambusae
Phyllostachys bambusoides Sieb. & Zucc. var. *bambusoides*
L. minoensis
L. phyllostachydis
Physalis pubescens L.
L. physalidis
Physostegia virginiana (L.) Benth.
L. physostegiae
Phyteuma scheuchzeri All.
L. psilospora
Phyteuma spicatum L.
L. phyteumatis
Phytolacca americana L.
L. clavigera
L. variegata
Phytolacca decandra L.
L. phytolaccae
Picris hieracioides L.
L. picridis
Pilularia sp.
L. pilulariae
Pimpinella anisum L.
L. pimpinellae
Pinecenectria sp.
L. almeidana
Pinus sylvestris L.
L. acicola
L. picastra
L. pini
Pinus sp.
L. squamata
Piper capense L.
L. piperis
Pircunia dioica Moq.
L. argentinensis
Pistacia terebinthus L.
L. emiliana
Placodium teicholytum (Ach.) DC.
L. crozalsii
Plantago alpina L.
L. winteri
Plantago cynops L.
L. cynops
Plantago macrostachys Decne.
L. austro-americana
Plantago maritima L.
L. vagabunda subsp. *alvarensis*
Plantago sp.
L. plantaginicola
Platanus occidentalis L.
L. platanicola
Platanus sp.
L. platanicola
Platychora ulmi (Schleich.:Fr.) Petrak
L. platychorae

Pleioblastus hindsii (Munro) Nakai
L. bambusae
Pleioblastus simoni (Carriere) Nakai
L. bambusae
Pleurospermum austriacum (L.) Hoffm.
L. ogilviensis var. *pleurospermi*
Plocama pendula W. Aiton
L. plocamae
Plumbago sp.
L. plumbaginis
Poa alpina L.
L. microscopica
Poa annua L.
L. muirensis
Poa aquatica L.
L. culmifraga var. *propinqua*
Poa colpodea Th. Fries
L. microscopica
Poa nemoralis L.
L. linearis
L. poae
Poa pratensis L.
L. avenaria
Poa sudetica Haenke
L. culmifraga forma *poae*
Poa sp.
L. sparsa
Poa sp.?
L. anarithmoides
Polygonatum sp.
L. polygonati
Polygonum bistorta L.
L. altaica
Polymmis sp.
L. doliolum
Polytrichum formosum Hedw.
L. heufleri
Polytrichum juniperinum Willd. ex Hedw. var. *alpinum* Schimp.
L. polytrichina
Populus alba L.
L. aegira
L. alcides
L. leucoplaca
Populus balsamifera L.
L. borealis var. *populi*
Populus nigra L.
L. salicinearum
Populus tremula L.
L. immunda
Populus sp.
L. decaisneana
Porella sp.
L. porellae
Potentilla argentea L.
L. minima
L. superficialis
Potentilla argyrophylla Wallich ex Lehm.
L. hollosiana
Potentilla caulescens L.
L. pulchra
Potentilla fragarioides L.
L. hollosiana
Potentilla maculata Pour.
L. oligotheca
Potentilla sp.
L. doliolum
Poterium sanguisorba L.
L. poterii
Primula elatior (L.) Hill
L. primulana
Primula latifolia Lapeyr.
L. primulaecola
Primula sikkimensis Hook.
L. delawayi
Protea melaleuca R. Br.
L. protearum
Prunella vulgaris L.
L. brunellae
L. hesperia
Prunus avium L.
L. rimicola
Prunus baccata Borkh.
L. corticola
Prunus domestica L.
L. corticola
L. pruni
Prunus dulcis (Mill.) D.A. Webb
L. pachytheca
Prunus mume Sieb. & Zucc.
L. mume
Prunus spinosa L.
L. corticola
L. lycii
Pseudosasa japonica (Siebold & Zucc. ex Steudel) Makino
L. bambusae
Pteridium aquilinum (L.) Kuhn
L. coorgica
Pteris aquilina L.
L. aquilina
Pterocelastrus tricuspidatus Walp.
L. pterocelastri
Punica granatum L.
L. puniciae
Pyrola secunda L.
L. marginata
Pyrus communis L.
L. lucilla
L. subcutanea
Pyrus sinensis Hort.
L. nashi
Quamoclidion multiflorum Torr. ex A. Gray
L. quamoclidii
Quercus pedunculata Ehrh.
L. dryadea
L. vagabunda
Quercus robur L.
L. alcides forma *quercina*
Quercus suber L.
L. scolecosporarum
Quercus virens Ait.
L. janus
Quercus sp.
L. dryophila
L. leucoplaca
L. puteana
Radicula sp. (=*Rorippa* sp.)
L. reidiana
Ramalina sp.
L. ramalinae
Ranunculus affinis R. Br.
L. ranunculi
Ranunculus nivalis L. var. *sulphureus* Wahlenberg
L. weberi
Ranunculus polyanthemos L.
L. ranunculi-polyanthemi
Ranunculus thora L.
L. thorae
Ranunculus villarsii DC.
L. andrijevicensis
Raphanus maritimus Sm.
L. raphani
Reseda lutea L.
L. resedae
Restio australis R. Br.
L. restionis
Rhamnus sp.
L. limitata
Rhinanthus sp.
L. affinis
L. dolioloides var. *rhinanthi*
Rhizocarpon geographicum (L.) DC.
L. geographicola
L. polaris
Rhodiola rosea L.
L. rhodiolicola
Rhododendron ferrugineum L.
L. rhododendri
Rhododendron sp.
L. californica
L. rhododendri
Rhus glabra L.
L. rhoina
Rhus typhina L.
L. curta
Ribes alpinum L.
L. cladophila
L. ribis
Ribes grossularia L.
L. grossulariae

Ribes nigrum L.
L. anceps
Ricinus communis L.
L. torrendii
Rinodina collectica (Flk.) Arn.
L. maheui
Robinia pseudacacia L.
L. eustoma forma *leguminosa*
L. lyndonvillae
L. petiolicola
Rosa canina L.
L. aculeorum
Rosa sp.
L. coniothyrium
L. corticola
L. fuscella
L. hazslinszkii
L. lejostega
L. sepincola
Rubia peregrina L.
L. bornmuelleri
L. icositana
Rubus fruticosus L.
L. coniothyrium
L. notarisii
Rubus idaeus L.
L. oxyspora
L. praetermissa
Rubus odoratus L.
L. praetermissa
Rubus sp.
L. abbreviata
L. controversa
L. doliolum
L. hendersoniae
L. osculanda
L. sepincola
L. thomasiana
L. vagabunda var. *sarmenti*
Rudbeckia amplexicaulis Vahl.
L. rudbeckiae
Rulingia prostrata Maiden & Betche
L. rulingiae
Rumex acetosa L.
L. quadriseptata
Rumex nepalensis Sprengel
L. rumicicola
L. rumicis
Rumex patientia L.
L. rumicis
Rumex scutatus L.
L. scutati
Rumex sp.
L. rumicis
L. sepincola
L. wegeliniana
Ruscus aculeatus L.
L. convallariae forma *rusci*
L. glauco-punctata
L. rusci
L. rusci forma *caulina*
L. ruscicola forma *cladodiicola*
Ruscus androgynus L.
L. rusci
Ruscus hypoglossum L.
L. rusci
L. rusci var. *rusci-hypoglossi*
Ruscus hypophyllum L.
L. rusci var. *hypophyllum*
Ruscus sp.
L. ruscicola
Ruta graveolens L.
L. bulgarica
Sabal serrulata Roem & Schult.
L. sabalicola
Sabal sp.
L. sabaligera
Saccharum officinarum L.
L. bicolor
L. kuangfuensis
L. sacchari
L. saccharicola
L. spegazzini
L. spegazzini var. *minor*
L. taiwanensis
L. tucumanensis
Sagittaria sp.
L. duplex
Salicornia peruviana H.B.K.
L. promontorii
Salix alba L.
L. salicinearum
Salix aurita L.
L. cinerea
Salix caprea L.
L. vagabunda forma *salicis-capreae*
Salix purpurea L.
L. purpurearum
L. vagabunda
Salix vitellina L.
L. coniothyrium
Salix sp.
L. baggei
L. borealis
L. consimilis
L. gillotiana
L. hendersoniae
L. leucoplaca
L. lonicerina
L. malojensis
L. xylogena
Salsola kali L.
L. kali
L. lecanora
L. salsolae
Salvia glutinosa L.
L. montana
Salvia officinalis L.
L. nicolai
L. salviae
Salvia pratensis L.
L. caespitosa forma *salviae*
Sambucus ebulus L.
L. derasa forma *macrospora*
L. dumetorum forma *ebuli*
L. megalospora
L. ruthenica
Sambucus melanocarpa A. Gray
L. sambucina
Sambucus nigra L.
L. coniothyrium
L. sambuci
Sambucus racemosa L.
L. dumetorum var. *dolichospora*
L. hirta
L. luxemburgensis var. *dolichospora*
L. tiroliensis
Sanguisorba officinalis L.
L. sanguisorbae
Sanguisorba polygama F. Nyl.
L. sanguisorbae
Sansevieria ehrenbergii Schweinf. ex Baker
L. baldratiana
Sarothamnus scoparius (L.) Wimmer ex Koch
L. fuscella forma *microspora*
L. sarothamni
Sarothamnus sp.
L. californica
Sarracenia purpurea L.
L. scapophila
Sasa paniculata (F. Schmidt) Makino
L. bambusae
Sasa sp.
L. sasacola
L. sasae
Sasaella ramosa (Makino) Makino
L. bambusae
Satureja hortensis L.
L. fallaciosa
Saxifraga oppositifolia L.
L. brachyasca
Saxifraga sp.
L. monotis
Scabiosa columbaria L.
L. modesta
L. passerinii
Scabiosa urceolata Desf.
L. obesa
Scheuchzeria palustris L.
L. bacillifera

Schoenocaulon officinale A. Gray
L. schoenocauli
Schoenoplectus lacustris (L.) Palla
L. lacustris
L. sowerbyi
Scirpus holoschoenus L.
L. apogon
L. holmii
L. micropogon
L. striolata
Scirpus lacustris L.
L. culmicola var. *aquatica*
L. maculans
L. scirpina
L. sowerbyi
Scirpus maritimus L.
L. saxonica
Scirpus sylvaticus L.
L. nardi var. *dubiosa*
Scirpus sp.
L. littoralis
L. maculans
L. michotii
Scrophularia aquatica L.
L. camilla
L. scrophulariae
Scrophularia canina L.
L. torbolensis
Scrophularia nodosa L.
L. oreophiloides subsp. *scrophulariae*
Scutellaria brevibracteata Stapf
L. davisiana
Secale cereale L.
L. secalina
L. secalis
L. setulosa
Secale sp.
L. pontiformis
Selaginella arenicola subsp. *acanthonota* (Underwood) R. Tryon
L. rostrata
Selaginella helvetica (L.) Spring
L. helvetica
L. helvetica forma *major*
L. lycopodiicola var. *major*
L. major
Selaginella rupestris (L.) Spring
L. rostrata
Selaginella underwoodii Hieron.
L. mellispora
Semele androgyna (L.) Kunth
L. semelina
Semiarundinaria tatebeana Muroi
L. bambusae
Senecio atratus Greene
L. clivensis
L. clivensis var. *constricta*
Senecio cordatus Koch
L. ogilviensis var. *senecionis-cordata*
Senecio crassulus A. Gray
L. octoseptata
Senecio erucifolius L.
L. rothomagensis
Senecio fuchsii C.C. Gmelin
L. dumetorum var. *coniformis*
Senecio jacobaea L.
L. derasa
L. modesta forma *jacobae*
L. ogilviensis
Senecio nemorensis L.
L. macrospora
L. robusta
L. senecionis
Senecio rupestris Waldst. & Kit.
L. robusta
Senecio vulgaris L.
L. dolioloides
Senecio sp.
L. clivensis
L. doliolum
Seseli montanum L.
L. montis-bardi
Seseli sp.
L. niessleana var. *staritzii*
Sieversia turbinata (Rydb.) Greene
L. sieversiae
Silene acaulis (L.) Jacq.
L. hausmanniana
L. hausmanniana var. *cherleriae*
L. sabauda
L. silenes-acaulis
Silene arvatica Lag.
L. sabauda forma *arvaticae*
Silene inflata Sm.
L. silvestris
Silene rosulata Soyer-Willem. & Godr.
L. indeprensa
Sinapis arvensis L.
L. sinapis
Sisymbrium alliaria (L.) Scop.
L. alliariae
Sisymbrium loeselii L.
L. submaculans
Sisymbrium strictissimum L.
L. acutispora
Smallanthus uvedalia (L.) Mackenzie
L. longipedicellata
Smilax aspera L.
L. aetnensis
L. catalaunica
L. smilacis
Smilax excelsa L.
L. dobrogica
Smilax mauritanica Poiret
L. papulosa
Smilax pseudo-china L.
L. nervisequa
Smilax sp.
L. doliolum
L. smilacis
Sobolewskia lithophila Bieb.
L. lithophilae
Solanum dulcamara L.
L. opizii
L. sarmenticia
L. solani
L. solanicola
L. umbrosa
L. vagabunda var. *dulcamarae*
Solanum sodomeum L.
L. sodomaea
Solanum sp.
L. comatella
Solidago caesia L.
L. longipedicellata
Solidago virgaurea L.
L. ogilviensis forma *megalospora*
L. planiuscula
Solidago sp.
L. aulica
L. doliolum
L. perplexa
L. solidaginis
Solorina crocea (L.) Ach.
L. lichenicola
L. oligospora
L. rivana forma *solorinae*
Sonchus sp.
L. doliolum
Sophora jabonica L.
L. sophorae
Sophora tetraptera J. Mill.
L. martinianum
Sorbaria sorbifolia A. Br.
L. spiraeae
Sorbus aucuparia L.
L. sorbi
Sorbus sp.
L. leucoplaca
Sorghum arundinaceum Roem & Schult.
L. sorgho-arundinacei
Sorghum vulgare Pers.
L. amphibola
L. culmifraga
L. eustoma
L. grisea
L. septovariata

Sparganium erectum L.
L. sparganii
Sparganium ramosum Hudson
L. huthiana
L. sparganii
L. sparsa var. *meizospora*
Sparganium sp.
L. clara
Spartina alterniflora Loisel.
L. neomaritima
Spartina juncea auct.
L. borziana
Spartina townsendii H. Groves & J. Groves
L. neomaritima
Spartina sp.
L. discors
L. duplex
L. incarcerata
L. macrosporidium
L. marina
L. neomaritima
L. pelagica
L. spartinae
L. sticta
Spartium junceum L.
L. lusitanica
Spartium sp.
L. dioica
Sphyridium fungiforme Flotow
L. sphyridiana
Spiraea sorbifolia L.
L. spiraeae
Sporobolus depauperatus Torr. ex Hemsl.
L. sporoboli
Staphylea trifolia L.
L. rubrotincta
Statice occidentalis Lloyd
L. staticicola
Steironema ciliatum (L.) Rafin.
L. steironematis
Stellaria graminea L.
L. isariphora
L. salebricola
Stellaria humifusa Rottb.
L. stellariae
Stellaria media (L.) Vill.
L. richoni
L. stellariae
Stellaria uliginosa Murray
L. uliginosa
Stenotaphrum secundatum (Walter) O. Kuntze
L. narmari
Stereocaulon alpinum Laur.
L. apocalypta
L. stereocaulorum
Stereum bicolor (Pers.) Pers.
L. stereicola
Stereum subpileatum Berkeley & Broome
L. fungicola
Stipa capillata L.
L. stipae
Stipa pennata L.
L. matritensis
Stipa tenacissima L.
L. macrochloae
L. pampaniniana
L. stipae
L. stipae-minor
Stratiotes aloides L.
L. stratiotis
Suaeda australis Moq.
L. suaedae
Succisa pratensis Moench.
L. planiuscula
Succisa sp.
L. modesta forma *succisae*
L. morthieriana
Swertia sp.
L. swertiae
Symphytum caucasicum Bieb.
L. dumetorum var. *symphyti*
Syringa vulgaris L.
L. trematostoma
Tamarix gallica L.
L. hollosii
L. meridionalis
L. tamaricis
Tamarix germanica L.
L. tamaricis
Tamarix sp.
L. crozalsiana
Tanacetum vulgare L.
L. dolioloides
L. tanaceti
L. thielensii
Taxus canadensis Marsh.
L. taxicola
Tecoma radicans Juss.
L. carpophila
Tellima grandiflora (Pursh) Douglas ex Lindley
L. deficiens
Tephrosia virginiana (L.) Pers.
L. tephrosiae
Teucrium scorodonia L.
L. teucrii
L. wegeliniana forma *teucrii*
Thalictrum aquilegifolium L.
L. tenuis
L. thalictri
L. thalictrina
Thalictrum collinum Wallr.
L. thalictricola
Thalictrum dioicum L.
L. houseana
Thalictrum flavum L.
L. cruenta
Thalictrum minus L.
L. quadriseptata
Thea sinensis L.
L. cavarae
L. hottai
Theobroma cacao L.
L. theobromicola
Thermopsis montana Nutt.
L. wehmeyeri
Thuja orientalis L.
L. thujaecola
Tilia sp.
L. leucoplaca
L. priuscheggiana
Tillandsia bicolor Brongn.
L. aerea
Tofieldia calyculata (L.) Wahlenb.
L. crastophila forma *tofieldiae*
L. oreophila
L. submodesta
L. tofieldiae
Tortula tortuosa Ehrh. ex Hedw.
L. bryophila
Tragopogon sp.
L. ophioboloides
Trevoa trinervia Gill. & Hook.
L. trevoae
Trichopteryx sp. [as *T. afroflammida*]
L. trichopterygis
Trifolium alpestre L.
L. trifolii-alpestris
Trifolium angustifolium L.
L. agnita var. *trifolii*
Trifolium kingii S. Wats.
L. monticola
Trifolium medium L.
L. trifolii
Trifolium trichocephalum Bieb.
L. balcarica
Triglochin maritima L.
L. hollosiana
L. juncaginearum
L. maritima
Triglochin palustris L.
L. juncaginearum
L. monilispora forma *triglochinis*
L. triglochinicola
L. triglochinis
Trisetum distichophyllum (Vill.) Beauv.
L. volkartiana
Trisetum longiglume Hackel
L. mendozana
Trisetum spicatum (L.) K. Richter
L. hollosiana
L. volkartiana

Trisetum subspicatum (L.) Beauv.
    L. microscopica
Triticum aestivum L.
    L. korrae
    L. narmari
Triticum durum Desf.
    L. avenaria form sp. *triticea*
Triticum repens L.
    L. rubelloides
Triticum vulgare Vill.
    L. avenaria form sp. *triticea*
    L. nodorum
    L. recutita
    L. tritici
Triticum sp.
    L. pontiformis
Trollius europaeus L.
    L. trollii
Typha angustata Bory & Chaub.
    L. aquatica
Typha angustifolia L.
    L. dematiicola
    L. iridigena var. *typhae*
    L. lacustris
    L. typharum
    L. typhiseda
    L. typhiseda forma *sodoloci*
Typha latifolia L.
    L. bispora
    L. caricis
    L. grandispora
    L. kunzeana
    L. lacustris
    L. licatensis
    L. licatensis forma *rupefortensis*
    L. maculans var. *typhicola*
    L. palustris
    L. perpusilla var. *typhae*
    L. pseudohleria
    L. punctillum
    L. typhae
    L. typharum
    L. typhicola
Typha sp.
    L. duplex
    L. mucosa
Ulmus campestris auct.
    L. massariella
    L. ulmicola
Ulmus sp.
    L. leucoplaca
    L. ramulicola
Umbellularia sp.
    L. odora
Umbilicaria pustulata (L.) Hoffm.
    L. umbilicariae
Urtica dioica L.
    L. acuta
    L. acuta forma *insignis*
    L. acuta forma *urticae*
    L. atropurpurea
    L. coniformis
    L. conoidea forma *macrospora*
Urtica sp.
    L. acutiuscula
    L. doliolum
Usnea florida (L.) Web.
    L. usneae
Vaccinium sp.
    L. lejostega
Valeriana dubia Turcz.
    L. dubia
Valeriana officinalis L.
    L. agnita
    L. carneomaculans
    L. quadriseptata
Veratrum sp.
    L. veratri
Verbascum phlomoides L.
    L. echinops
Verbesina virginica L.
    L. drechsleri
Veronica latifolia auct.
    L. striata
Veronica urticifolia Jacq.
    L. carpogena
Veronica sp.
    L. doliolum
Viburnum tinus L.
    L. tini
Vicia cracca L.
    L. viciae
Vicia sativa L.
    L. niessleana forma *viciae*
Vinca major L.
    L. maderensis
Vinca media Hoffmanns. & Link
    L. demissa
Vinca minor L.
    L. vincae
Vincetoxicum officinale Moench
    L. molybdina
Vincetoxicum sp.
    L. scotophila
Vitex agnus-castus L.
    L. casta
Vitis vinifera L.
    L. ampelina
    L. cerlettii
    L. chaetostoma
    L. cirricola
    L. cookei
    L. gibelliana
    L. pampini
    L. socia
    L. vinealis
    L. viticola
    L. vitigena
    L. vitis
Vitis vinifera L. subsp. *sylvestris*
    L. sclavonica
Vitis sp.
    L. pampini
Vriesea sp.
    L. vrieseae
Xanthoxylum sp.
    L. brasiliensis
Xerophyllum asphodeloides (L.) Nutt.
    L. xerophylli
Xerophyllum tenax (Pursh) Nutt.
    L. hysterioides
Yucca elephantipes
    L. setosa
Yucca filamentosa L.
    L. filamentosa
Yucca gloriosa L.
    L. obtusispora
Yucca sp. [as *Y. colusplei*]
    L. pacifica
Zea mays L.
    L. bubakii
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    L. maydis
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    L. punctiformis
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L. fuscidula forma *magnolii*
L. gaubae
L. georgius-fischeri
L. gigaspsora
L. glandulosae
L. glauco-punctata
L. glyceriae
L. glyceriae-plicatae
L. gossypii
L. graminum
L. grandispora
L. gratissima
L. gratissima var. *longispora*
L. guazumae
L. gynerii
L. hardenbergiae
L. hausmanniana
L. hausmanniana var. *cherleriae*
L. hederae
L. hedericola
L. helicicola
L. heloniaefolia
L. helvetica
L. hemicrypta
L. hermodactyli
L. hesperia
L. heveae
L. honiaraensis
L. huthiana
L. hyperborea
L. hysterioides
L. immunda
L. indeprensa
L. indica
L. infernalis
L. insignis
L. insignis forma *airae-cespitosae*
L. iridicola
L. iridigena
L. iridigena var. *typhae*
L. iridis
L. isariphora
L. iwamotoi
L. jahnii
L. janus
L. jubaeae
L. junci
L. juncina forma *macrospora*
L. juniperina
L. kerguelensis
L. kotschyana
L. lacustris
L. larseniana
L. lasioderma
L. lathonia var. *hellbori-foetidi*
L. lauri
L. leersiae
L. leersiana
L. licatensis
L. licatensis forma *rupefortensis*
L. lilii
L. lingue
L. livida
L. lobeliae
L. lucilla
L. lucina
L. luzulae
L. maclurae
L. macrochloae
L. macrotheca
L. maculans
L. magnoliae
L. magnusiana
L. major
L. malojensis
L. mandshurica
L. marantae
L. marcyensis
L. marginalis
L. marginata
L. maritima
L. matritensis
L. maydis
L. media
L. melicae
L. mellispora
L. mendozana
L. mertensiae
L. microscopica subsp. *calami*
L. microscopica var. *alpina*
L. mikaniae
L. minima
L. miyakeana
L. molleriana
L. monticola
L. morthieriana
L. moutan
L. mucosa
L. muirensis
L. muricata
L. musae
L. musarum
L. musigena
L. nardi var. *dubiosa*
L. nashi
L. neglecta
L. nervisequa
L. nesodes
L. niessleana
L. nobilis
L. nodorum form sp. *hordei*
L. obtusispora
L. obtusispora forma *agaves*
L. occulta
L. oligotheca
L. ophiopogonis
L. ophiopogonis var. *graminum*
L. orthrosanthi
L. oryzae
L. pachyasca
L. pachytheca
L. pacifica
L. paludosa
L. pampaniniana
L. pandani
L. pandanicola
L. panici
L. paoluccii
L. papulosa
L. paraguariensis
L. parvula
L. parvula var. *iridis-germanicae*
L. passerinii
L. pelargonii
L. penniseticola
L. perforans
L. petri
L. phlogis
L. phoradendri
L. phormii
L. physalidis
L. pilulariae
L. piperis
L. plantaginicola
L. plemeliana
L. pomona
L. portoricensis
L. primulaecola
L. priuscheggiana
L. protearum
L. pruni

L. pruni forma *plurivora*
L. pterocelastri
L. puccinioides
L. puiggarii
L. pulchra
L. punctillum
L. purpurearum
L. pusilla
L. puttemansii
L. recutita
L. rehmiana
L. rehmii
L. rhododendri
L. rivalis
L. rostrata
L. rostrupii
L. rusci
L. rusci forma *fourcroyae*
L. rusci var. *rusci-hypoglossi*
L. ruscicola
L. sabauda
L. sabauda forma *arvaticae*
L. sabuletorum
L. sacchari
L. saccharicola
L. saginata
L. salebricola
L. salicinearum
L. sasae
L. scolecosporarum
L. seriata
L. silenes-acaulis
L. smarodsii
L. smilacis
L. solani
L. sorbi
L. sorghi-arundinacei
L. sparsa
L. sparsa var. *meizospora*
L. spegazzini
L. staticicola
L. stellariae
L. stipae
L. stipae-minor
L. stratiotis
L. striolata var. *caricis-glaucae*
L. subiculifera
L. substerilis
L. subtecta
L. swertiae
L. sylvatica
L. taichungensis
L. taiwanensis
L. tanaceti
L. taxicola
L. theobromicola
L. thorae
L. thujaecola
L. tini
L. tofieldiae
L. tonduzi
L. translucens
L. trifolii-alpestris
L. tritici
L. typharum
L. typharum subsp. *phragmatina*
L. typhicola
L. typhiseda
L. typhiseda forma *sodoloci*
L. uliginosa
L. ulmicola
L. vagans
L. vagans forma *scirpi*
L. valdobbiae
L. vanhoeffeniana
L. variiseptata
L. vectis
L. verwoerdiana
L. vincae
L. vinosa
L. vrieseae
L. weberi
L. williamsii
L. winteri
L. woodrow-wilsonii
L. xerophylli
L. xiphii
L. yulan
L. zeae
L. zeae-maydis
L. zeicola
L. zingiberis

Nuts
L. cacuminispora

Paper
L. fibrincola
L. papyricola
L. tritici var. *papyricola*
L. typharum subsp. *papyrogena*

Pedicels
L. eranthemi
L. eustoma

Peduncles
L. bryzae
L. espeletiae
L. francoae
L. lycopodiicola
L. papyri
L. raphidophora
L. scapophila
L. typhiseda
L. vitensis

Petioles
L. anemones
L. cinclidoti
L. eryngii
L. monticola
L. petiolaris
L. petiolicola
L. phoenicis
L. primulaecola
L. typhiseda

Pods
L. endiusae
L. eustoma forma *leguminosa*
L. impressa
L. lunariae
L. lyndonvillae

Rachis
L. culmifraga forma *poae*
L. eustomoides forma *lolii*
L. sabalicola
L. trochus

Rhizomes
L. culmicola var. *rhizomatum*
L. heterospora
L. littoralis
L. pontiformis
L. rhizomatum
L. vagabunda subsp. *alvarensis*

Roots
L. australiensis
L. capparidis
L. circinans
L. cladii
L. lycii
L. maculans forma *denudata*
L. septovariata

Runners
L. cookei
L. grignonnensis
L. haematites
L. nectrioides
L. notarisii
L. pampini
L. pleosporoides
L. rhizomatum
L. rimalis
L. sarmenticia
L. thomasiana
L. vagabunda var. *sarmenti*
L. vinealis
L. vitalbae

Seeds
L. albo-punctata
L. microscopica forma *glyceriae*
L. sequana
L. woroninii

Sepals
L. auerswaldii
L. sepalorum

Sheaths
- *L. altaica*
- *L. arenaria*
- *L. avenaria* form sp. *triticea*
- *L. cariciphila*
- *L. cattanei*
- *L. cookei*
- *L. culmicola* forma *melicae*
- *L. culmicola* var. *hispalensis*
- *L. culmicola* var. *nigrans*
- *L. culmorum*
- *L. fuckelii* forma *filamentifera*
- *L. interspersa*
- *L. korrae*
- *L. lagenoides*
- *L. latebrosa*
- *L. matritensis*
- *L. media*
- *L. monilispora*
- *L. narmari*
- *L. neomaritima*
- *L. nigrans*
- *L. nodorum* form sp. *hordei*
- *L. notarisii*
- *L. pandani*
- *L. rivalis*
- *L. rousseliana*
- *L. sacchari*
- *L. salvinii*
- *L. spartii*
- *L. spegazzini*
- *L. subalpina*
- *L. vaginae*

Sporangia
- *L. heufleri*

Stems
- *L. abbreviata*
- *L. acanthi*
- *L. achilleae*
- *L. aconiti*
- *L. aculeorum*
- *L. acuta*
- *L. acuta* forma *insignis*
- *L. acuta* forma *urticae*
- *L. acutispora*
- *L. acutiuscula*
- *L. affinis*
- *L. agminalis*
- *L. agnita*
- *L. agnita* subsp. *labens*
- *L. agnita* var. *ambigua*
- *L. agnita* var. *bupleuri*
- *L. agnita* var. *chrysanthemi*
- *L. agnita* var. *erigerontis*
- *L. agnita* var. *major*
- *L. agnita* var. *trifolii*
- *L. albulae*
- *L. alliariae*
- *L. allorgei*
- *L. amphibola*
- *L. anacycli*
- *L. anarrhini*
- *L. andrijevicensis*
- *L. anomala*
- *L. anthelmintica*
- *L. antherici*
- *L. anthostomoides*
- *L. aparines*
- *L. aquilana*
- *L. aquilegiae*
- *L. arabidis*
- *L. argentina*
- *L. artemisiae*
- *L. arthrophyma*
- *L. arunci*
- *L. arvensis*
- *L. asclepiadis*
- *L. asparagi*
- *L. asparagina*
- *L. astericola*
- *L. asteris*
- *L. atropurpurea*
- *L. aucta*
- *L. aulica*
- *L. balcarica*
- *L. ballotae*
- *L. bardanae*
- *L. bellynckii*
- *L. berlesei*
- *L. blumeri*
- *L. bocconiae*
- *L. boucera*
- *L. brachyasca*
- *L. brachysperma*
- *L. brauni*
- *L. bresadolaeana*
- *L. brightonensis*
- *L. brunellae*
- *L. bryophila*
- *L. bubakii*
- *L. buddlejae*
- *L. bulgarica*
- *L. bupleuri*
- *L. caballeroi*
- *L. cadubriae*
- *L. caespitosa*
- *L. caespitosa* forma *salviae*
- *L. calvescens*
- *L. camphorata*
- *L. canadensis*
- *L. carduorum*
- *L. carlinoides*
- *L. carneomaculans*
- *L. cassiaecola*
- *L. castilleiae*
- *L. castillejae*
- *L. caulincola*
- *L. centaureae*
- *L. centrafricana*
- *L. cephalariai-uralensis*
- *L. cerastii*
- *L. ceratispora*
- *L. cerei-peruviani*
- *L. cervispora*
- *L. cesatiana*
- *L. chelidonii*
- *L. chrysanthemi*
- *L. cibostii*
- *L. circinans*
- *L. cirricola*
- *L. cladophila*
- *L. clavata*
- *L. clavigera*
- *L. clavispora*
- *L. clivensis*
- *L. clivensis* var. *constricta*
- *L. coleosanthi*
- *L. collinsoniae*
- *L. comatella*
- *L. complanata*
- *L. compositarum*
- *L. compressa*
- *L. concinna*
- *L. conferta*
- *L. congesta*
- *L. coniformis*
- *L. conii*
- *L. coniigena*
- *L. coniothyrium*
- *L. conoidea*
- *L. conoidea* forma *angelicae*
- *L. conoidea* forma *asteris*
- *L. conoidea* forma *macrospora*
- *L. consessa*
- *L. controversa*
- *L. convallariae*
- *L. coorgica*
- *L. corallorhizae*
- *L. cornuta*
- *L. coronillae*
- *L. corticola*
- *L. corynispora*
- *L. cosmicola*
- *L. crastophila* forma *tofieldiae*
- *L. cruenta*
- *L. crustacea*
- *L. cucurbitarioides*
- *L. culmicola* forma *major*
- *L. culmifraga* var. *bromicola*
- *L. culmifraga* var. *linearis*
- *L. curta*
- *L. cylindrospora*
- *L. cylindrostoma*
- *L. cynoglossi*
- *L. cynops*
- *L. darkeri*

L. davidii
L. davisiana
L. dearnessii
L. deficiens
L. delawayi
L. dematiicola
L. dematium
L. demissa
L. depressa
L. derasa forma *alpestris*
L. derasa forma *robusta*
L. derasa var. *franconica*
L. desciscens
L. dianthi
L. diaporthoides
L. digitalis
L. dissiliens
L. dolioloides
L. dolioloides var. *cirsii*
L. dolioloides var. *inops*
L. dolioloides var. *lathyri*
L. dolioloides var. *rhinanthi*
L. doliolum
L. doliolum forma *carlinae-vulgaris*
L. doliolum forma *syndoliola*
L. doliolum var. *angustispora*
L. doliolum var. *cacaliae*
L. doliolum var. *dissimilis*
L. doliolum var. *leonuri*
L. doliolum var. *pachyspora*
L. doliolum var. *pinquicula*
L. doliolum var. *subdisticha*
L. drabae
L. dryadea subsp. *lussoniensis*
L. dryadis
L. dubia
L. dumetorum
L. dumetorum forma *ebuli*
L. dumetorum forma *meliloti*
L. dumetorum var. *coniformis*
L. dumetorum var. *coronillae*
L. dumetorum var. *galii-borealis*
L. dumetorum var. *marrubii*
L. dumetorum var. *symphyti*
L. eburnea
L. echiella
L. echii
L. echinella
L. echinops
L. ellisiana
L. elongata
L. endiusae
L. epilobii
L. equiseti
L. equiseticola
L. erigerontis
L. eriophora
L. eryngii
L. ettalensis
L. euphorbiae
L. euphorbiae forma *esulae*
L. euphorbiaecola
L. eutypoides
L. faginea
L. fallaciosa
L. fallax
L. ferruginea
L. ferulicola
L. filiformis
L. fimbriata
L. fiumana
L. foeniculacea
L. foeniculacea subsp. *lupina*
L. foeniculi
L. fraserae
L. frondis
L. fuckelii
L. fuegiana
L. fulgida
L. galeobdolonis
L. galeopsidicola
L. galii
L. galiicola
L. galiicola var. *brachyspora*
L. galii-silvatici
L. galiorum
L. galiorum forma *cirsiorum*
L. galiorum forma *gentianae*
L. galiorum subsp. *antirrhini*
L. galiorum var. *gnaphaliana*
L. galiorum var. *lapsanae*
L. gaultheriae
L. genistae var. *microspora*
L. gigaspora
L. gloeospora
L. gnaphalii
L. grammodes
L. gypsophilae
L. haematites
L. harknessianna
L. helianthemi
L. heliopsidis
L. helminthospora forma *crithmi-maritimi*
L. hemerocallidis
L. hesperidicola
L. hiemalis
L. hirta
L. hollosiana
L. holmii
L. houseana
L. hrubyana
L. hurae
L. hyalospora
L. hyparrheniae
L. hyperici
L. icositana
L. incarcerata
L. incruenta
L. inculta
L. indica
L. insulana
L. jaceae
L. jacksonensis
L. jacksonii
L. johansonii
L. juncaginearum
L. junci-glauci
L. juncorum
L. kali
L. kalmiae
L. kalmusii
L. kochiana
L. kunzeana
L. lacustris
L. ladina
L. lankeana
L. larseniana
L. lasiosphaerioides
L. lassenensis
L. lathyri
L. lathyrina
L. lecanora
L. leptospora
L. lespedezae
L. lethalis
L. libanotis
L. limosa
L. lindquistii
L. lithophilae
L. lobayensis
L. longchampsi
L. longipedicellata
L. longispora
L. lonicerina
L. lophanthi
L. lupini
L. lupinicola
L. lusitanica
L. lyciophila
L. lythri

L. macrospora
L. macrosporidium
L. maculans
L. maculans var. *typhicola*
L. maderensis
L. malyi
L. maritima
L. marram
L. martagoni
L. massariella var. *disticha*
L. massarioides
L. media
L. medicaginicola
L. medicaginis
L. medicaginum
L. megalospora
L. melanommoides
L. melicae
L. meliloti
L. menthae
L. mesoedema
L. metasequoiae
L. microspora
L. microthyrioides
L. millefolii
L. mirabilis
L. modesta
L. modesta forma *digitalis-luteae*
L. modesta forma *jacobaeae*
L. modesta forma *lappae*
L. modesta forma *succisae*
L. modesta forma *sylvestris*
L. modesta var. *cibostii*
L. modesta var. *rubellula*
L. modestula
L. molluginis
L. molybdina
L. monilispora
L. monilispora forma *triglochinis*
L. montana
L. montis-bardi
L. morierae
L. muehlenbeckiae
L. multiseptata
L. multiseptata forma *alpina*
L. muralis
L. muscari
L. nanae
L. napelli
L. napi
L. nicolai
L. niessleana
L. niessleana forma *viciae*
L. niessleana var. *staritzii*
L. nigrella
L. nigricans
L. nigromaculata
L. nitschkei
L. nitschkei forma *adenostylidis*
L. norfolcia
L. norvegica
L. obesa
L. obesula
L. obiones
L. obiones var. *evolutior*
L. ocellata
L. ocimicola
L. octophragmia
L. octophragmia var. *major*
L. octoseptata
L. ogilviensis
L. ogilviensis forma *achilleae*
L. ogilviensis forma *lepidii*
L. ogilviensis forma *megalospora*
L. ogilviensis forma *myrrhis-odorata*
L. ogilviensis var. *pleurospermi*
L. ogilviensis var. *senecionis-cordati*
L. olericola
L. olivacea
L. onagrae
L. onobrychidicola
L. onobrychidis
L. ophioboloides
L. opizii
L. opuntiae
L. orchidearum
L. oreophila
L. oreophiloides
L. oreophiloides subsp. *scrophulariae*
L. ornithogali
L. orthogramma
L. oubanguiensis
L. owaniae
L. oxyriae
L. oxyspora
L. palustris
L. papaveris
L. parietariae
L. parietariae forma *lamii*
L. passeriniana
L. passerinii
L. pellita
L. penicillus
L. perplexa
L. perpusilla
L. personata
L. phaeospora
L. phaseoli
L. phaseolorum
L. physostegiae
L. phyteumatis
L. phytolaccae
L. pimpinellae
L. planiuscula
L. planiuscula forma *cruciferarum*
L. platanicola
L. platypus
L. plectrospora
L. plumbaginis
L. plurisepta
L. politis
L. polygonati
L. pomiformis
L. poterii
L. praeclara
L. pramontorii
L. pratensis
L. primulana
L. proliferae
L. pseudo-diaporthe
L. pseudohleria
L. psilospora
L. ptarmicae
L. pulchra
L. punctoidea
L. punjabensis
L. purpurea
L. quadriseptata
L. quamoclidii
L. ramsaugiensis
L. ranunculi
L. ranunculi-polyanthemi
L. ranunculoides
L. recessa
L. resedae
L. restionis
L. rhodiolicola
L. rhopalispora
L. rhopographoides
L. richoni
L. riofrioi
L. rivalis
L. rivularis
L. robusta
L. rostrupii
L. rothomagensis
L. rothomagensis var. *artemisiae*
L. rubellula
L. rubicunda
L. rudbeckiae
L. rugosa
L. rumicicola
L. rumicis
L. ruscicola
L. ruscicola forma *cladodiicola*
L. russellii

L. rustica
L. ruthenica
L. saccardiana
L. sacculus
L. salebrosa
L. salicaria
L. salsolae
L. sanguisorbae
L. sapeyensis
L. sarraziniana
L. schoenocauli
L. scitula
L. scotophila
L. scutati
L. semelina
L. senecionis
L. sepincola
L. septemcellulata
L. serbica
L. setosa
L. shahvarica
L. shastensis
L. sibirica
L. sibtorpii
L. sieversiae
L. sileris
L. silvestris
L. simmonsii
L. sinapis
L. slovacica
L. socialis
L. sodomaea
L. solani
L. solanicola
L. solidaginis
L. sparganii
L. spectabilis
L. staritzii
L. steironematis
L. stellariae
L. stellata
L. stictostoma
L. striata
L. striolata
L. subcaespitosa
L. subconica
L. submaculans
L. submodesta
L. subriparia
L. suffulta
L. surculorum
L. tanaceti
L. taurica
L. tenera
L. tenuis
L. tephrosiae
L. tetonensis
L. teucrii
L. thalictri
L. thalictricola
L. thalictrina
L. thielensii
L. thuemeniana
L. tolgorensis
L. torbolensis
L. torulispora
L. trichostoma
L. trifolii
L. triglochinicola
L. triglochinis
L. trimera
L. trimerioides
L. tritorulosa
L. trollii
L. tupae
L. typharum
L. uncinata
L. utahensis
L. vagabunda
L. vagabunda forma *abietis*
L. vagabunda forma *citri-limonii*
L. vagabunda forma *lonicerae*
L. vagabunda forma *salicis-capreae*
L. vagabunda var. *caulium*
L. vagabunda var. *dulcamara*
L. vahlii
L. valdiviensis
L. valesiaca
L. variegata
L. veratri
L. viciae
L. vindobonensis
L. vinosa
L. virginica
L. viridella
L. vitalbae var. *sarmenticola*
L. wegeliniana
L. wegeliniana forma *teucrii*
L. wehmeyeri
L. zahlbruckneri
L. zizaniaecola

Stolons
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L. hendersoniae
L. hermodactyli
L. herpotrichoides
L. heterospora
L. heufleri
L. hiemalis
L. hippophaes
L. hyalospora
L. hydrophila
L. involucralis
L. ischaemi
L. juncicola
L. kochiana
L. lamprocarpi
L. lathonia
L. lathonia var. *hellebori-foetidi*
L. lathyri
L. lathyrina
L. leersiae
L. leersiana
L. leptospora
L. licatensis
L. lichenicola
L. littoralis
L. littoralis forma *calamagrostidis-arenariae*
L. livida
L. lucilla
L. lucina
L. luctuosa
L. luzulae
L. maculans
L. magnusiana
L. major
L. mamillula
L. marginalis
L. marginata
L. massariella
L. massariella var. *disticha*
L. massarioides
L. medicaginis
L. medicaginum
L. melicae
L. meridionalis
L. michotii
L. micropogon
L. microscopica
L. microscopica var. *alpina*
L. mirandae
L. modesta var. *cibostii*
L. molluginis
L. monotis
L. montana
L. multiseptata forma *alpina*
L. nectrioides
L. neglecta
L. nigrans
L. nobilis
L. notarisii
L. ogilviensis
L. ogilviensis var. *senecionis-cordati*
L. ophiopogonis
L. oryzae
L. pampini
L. pandani
L. paoluccii
L. parietariae
L. parvula var. *iridis-germanicae*
L. passeriniana
L. passerinii
L. patellaeformis
L. peltigerarum
L. penicillus
L. perforans
L. perpusilla
L. petiolicola
L. phytolaccae
L. pinnarum
L. pinnarum var. *rachidis*
L. platycarpa
L. pomona
L. poterii
L. puccinioides
L. punctiformis
L. pycnostigma var. *morbosa*
L. pyrenopezizoides
L. ranunculoides
L. recessa
L. rehmii
L. resedae
L. rhizomatum
L. rhododendri
L. rhodophaea
L. rivana
L. rivana var. *solorinae*
L. rusci
L. rusci forma *caulina*
L. rusci forma *rusci-hypoglossi*
L. sacculus
L. salicaria
L. salicinearum
L. salviae
L. salvinii
L. sambuci
L. scirpina
L. scotophila
L. seriata
L. sicula
L. silenes-acaulis
L. sileris
L. socia
L. sodomaea
L. spartii
L. spatharum
L. stereocaulorum
L. striclata
L. subarticulata
L. subtecta
L. suffulta
L. sylvatica
L. thalictri
L. torbolensis
L. trichostoma
L. trimera
L. tritici
L. typharum
L. typhicola
L. ulmicola
L. vagabunda
L. vagabunda forma *critri-limonii*
L. vagabunda var. *divergens*
L. vagabunda var. *sarmenti*
L. vaginae
L. valdobbiae
L. vincae
L. vinealis
L. xiphii
L. xylogena
L. yulan

Ivory Coast
L. coffeigena var. *longirostrata*
L. petri
L. sorgho-arundinacei

Jamaica
L. peltigerea

Japan
L. akagiensis
L. apios
L. apios-fortunei
L. asperellae
L. bambusae
L. buddlejae
L. cinnamomi
L. hottai
L. inecola
L. japonica
L. lelebae
L. lilicola
L. minoensis
L. mume
L. nandinae
L. nashi
L. oryzicola
L. phyllostachydis
L. sasacola
L. sasae
L. thujaecola
L. tigrisoides
L. zizannivora

Java
- *L. sacchari*
- *L. trochus*

Kenya
- *L. bicolor*
- *L. nodorum*
- *L. tritici*

Kerguelen Island
- *L. kerguelensis*

Korea
- *L. iwamotoi*

Libya
- *L. pampaniniana*

Luxembourg
- *L. caespitosa* forma *salviae*
- *L. cerastii*
- *L. culmorum* var. *flavobrunnea*
- *L. dolioloides* var. *lathyri*
- *L. dolioloides* var. *rhinanthi*
- *L. dumetorum* var. *coniformis*
- *L. dumetorum* var. *dolichospora*
- *L. dumetorum* var. *symphyti*
- *L. echiella*
- *L. echii*
- *L. epicalamia* var. *pleosporoides*
- *L. euphorbiae* forma *esulae*
- *L. fuscella* var. *hippophaes*
- *L. galeobdolonis*
- *L. hemerocallidis*
- *L. iridigena* var. *typhae*
- *L. junci*
- *L. longispora*
- *L. luxemburgensis* var. *dolichospora*
- *L. microthyrioides*
- *L. monilispora* forma *triglochinis*
- *L. oxyspora*
- *L. paludosa*
- *L. petiolaris*
- *L. phyteumatis* forma *knautiae*
- *L. planiuscula* forma *succisae*
- *L. plectrospora*
- *L. proliferae*
- *L. rivalis*
- *L. silvestris*
- *L. sparsa* var. *meizospora*
- *L. trematostoma*
- *L. trifolii*
- *L. vitalbae* var. *sarmenticola*
- *L. wegeliniana* forma *teucrii*

Madeira Archipelago
- *L. maderensis*

Malaysia
- *L. scabiens*

Mauritania
- *L. tompkinsii*

Morocco
- *L. elaoudi*
- *L. gratissima*
- *L. gratissima* var. *longispora*
- *L. maheui*

Netherlands
- *L. ammophilae*
- *L. cariciphila*
- *L. desciscens*
- *L. donacina*
- *L. galiicola*
- *L. genistae*
- *L. hemicrypta*
- *L. junci*
- *L. periclymeni*
- *L. phlogis*
- *L. pseudo-diaporthe*
- *L. rhopographoides*
- *L. rousseliana*
- *L. stratiotis*

New Caledonia
- *L. australis*

New Zealand
- *L. martinianum*
- *L. reidiana*
- *L. typharum*

Nigeria
- *L. elaeidis*

Norway
- *L. andromedae*
- *L. caricinella*
- *L. consobrina*
- *L. dryadis*
- *L. dumetorum* var. *galiiborealis*
- *L. hyperborea*
- *L. insignis*
- *L. junciseda*
- *L. quadriseptata*
- *L. rostrupii*
- *L. sepalorum*
- *L. vagans*

Pakistan
- *L. abutilonis*
- *L. ahmadii*
- *L. depressa*
- *L. euphorbiicolla*
- *L. punjabensis*
- *L. rumicicola*
- *L. rumicis*

Philippines
- *L. ambiens*
- *L. amphiloga*
- *L. chusqueae*
- *L. dryadea* subsp. *lussoniensis*
- *L. erythrinae*
- *L. marantae*
- *L. oryzina*
- *L. panici*
- *L. simillima*
- *L. tungurahuensis*

Poland
- *L. alliariae*
- *L. caricina*
- *L. cerei-peruviani*
- *L. coniformis*
- *L. crustacea*
- *L. lycopodina*
- *L. norvegica*
- *L. opizii*
- *L. sowerbyi*
- *L. trifolii-alpestris*
- *L. triglochinis*
- *L. typhiseda*

Portugal
- *L. algarbiensis*
- *L. almeidae*
- *L. almeidana*
- *L. aloes*
- *L. anacycli*
- *L. anarrhini*
- *L. arbuti*
- *L. arecae*
- *L. buxina*
- *L. cisticola*
- *L. cocoes*
- *L. congesta*
- *L. conimbricensis*
- *L. coniothyrium*
- *L. convallariae* forma *dracaenae*
- *L. convallariae* forma *rusci*
- *L. daphnes*
- *L. demissa*
- *L. diaporthoides*
- *L. dolioloides*
- *L. dracaenae*
- *L. foeniculi*
- *L. holmii*
- *L. infernalis*
- *L. junci-acuti*
- *L. juncina*
- *L. lavandulae*
- *L. lusitanica*
- *L. maculans*
- *L. michotii*
- *L. molleriana*
- *L. nervisequa*
- *L. papillosa*
- *L. rusci*
- *L. rusci* var. *fourcroyae*
- *L. schoenocauli*
- *L. scolecosporarum*

L. thuemeniana
L. torrendii
L. translucens
L. vagabunda forma *daphnes*

Puerto Rico
L. portoricensis

Romania
L. acutispora
L. alexandrinis
L. derasa var. *franconica*
L. dobrogica
L. doliolum forma *carlinae-vulgaris*
L. doliolum var. *dissimilis*
L. doliolum var. *leonuri*
L. fuckelii
L. fusispora var. *erysimi*
L. glyceriae-plicatae
L. hazslinszkii
L. pomona
L. ranunculi-polyanthemi
L. salviae forma *minor*
L. woroninii

São Tomé
L. fungicola
L. musarum

Scandinavia
L. dolioloides
L. inarensis

Senegal
L. senegalensis

Sierra Leone
L. penniseticola

Solomon Islands
L. honiaraensis

South Africa
L. africana
L. caffra
L. cervispora
L. collumiae
L. owaniae
L. protearum
L. pterocelastri
L. verwoerdiana

Spain
L. agnita var. *trifolii*
L. caballeroi
L. carlinoides
L. catalaunica
L. cavanillesii
L. ceballosi
L. cirsii-arvensis
L. cistina
L. colocasiae
L. culmicola var. *hispalensis*
L. cynosuri
L. dolioloides
L. draconis
L. fuscidula forma *magnolii*
L. glyceriae
L. grossulariae
L. hispanica
L. junci-glauci
L. martagoni
L. matritensis
L. octophragmia
L. riofrioi
L. riparia
L. ruscicola forma *cladodiicola*
L. sabauda forma *arvaticae*
L. semelina
L. staticicola
L. striolata
L. variabilis
L. vitensis

Sri Lanka
L. depressa
L. lankeana
L. nesodes
L. smilacis
L. tornatospora

St. Thomas Island
L. musarum

Sweden
L. associata
L. bellynckii
L. caricis
L. cladophila
L. compressa
L. culmifraga
L. culmifraga forma *minuscula*
L. culmorum
L. doliolum
L. doliolum var. *subdisticha*
L. duplex
L. fuckelii
L. hendersoniae
L. hirta
L. jaceae
L. lasiosphaerioides
L. macrotheca
L. microscopica
L. nardi
L. nigrans
L. picastra
L. sepincola
L. solani
L. solanicola
L. vagabunda subsp. *alvarensis*

Switzerland
L. agnita var. *major*
L. albulae
L. blumeri
L. brauni
L. caricicola
L. caricis
L. centaureae
L. cladii
L. compositarum
L. cornuta
L. corticola
L. crucheti
L. culmorum
L. didymellae-vincetoxici
L. epicalamia
L. epilobii
L. eustoma
L. franconica
L. fuckelii
L. galii
L. galiorum var. *gentianae*
L. hippophaes
L. johansonii
L. juncicola
L. lacustris
L. ladina
L. libanotis
L. linearis
L. lycopodina
L. maculans
L. morthieriana
L. nanae
L. napelli
L. nardi
L. nigrans
L. nodorum
L. ocellata
L. ogilviensis
L. ophioboloides
L. palustris
L. parvula
L. petkovicensis
L. phacae
L. phaeospora
L. phyteumatis
L. pini
L. planiuscula
L. platychorae
L. pleurospora
L. polygonati
L. primulaecola
L. recutita
L. rimalis
L. rimicola
L. robusta
L. rousseliana
L. rumicis
L. septemcellulata
L. sowerbyi
L. sparsa
L. submodesta
L. sylvatica
L. taminensis
L. tenuis
L. thurgoviensis

L. tofieldiae
L. triglochinicola
L. trollii
L. typhicola
L. valesiaca
L. viciae
L. vitalbae
L. volkartiana
L. wegeliniana

Taiwan
L. coicis
L. kuangfuensis
L. musae
L. musigena
L. pandanicola
L. taichungensis
L. taiwanensis

Tanzania
L. elaeidicola

Tunisia
L. macrochloae
L. rothomagensis var. *artemisiae*
L. stipae-minor

Turkey
L. davisiana
L. dodonaeae
L. melicae
L. sylvatica

U.S.A.
L. acuta
L. agnita subsp. *labens*
L. agnita var. *erigerontis*
L. anomala
L. anthelmintica
L. arctalaskana
L. arthrophyma
L. arunci
L. asclepiadis
L. asparagi
L. associata
L. astericola
L. asteris
L. aulica
L. avenaria
L. avicenniae
L. beaumontii
L. berlesei
L. bicuspidata
L. bocconiae
L. borealis
L. borealis var. *populi*
L. boucera
L. brightonensis
L. byssincola
L. cacuminispora
L. californica
L. caricis
L. cassiaecola
L. castilleiae
L. castillejae
L. castrensis
L. caulincola
L. ceanothi
L. ceratispora
L. cercocarpi
L. chrysanthemi
L. clavicarpa
L. clavigera
L. clavispora
L. clivensis var. *constricta*
L. coleosanthi
L. collinsoniae
L. comatella
L. complanata
L. compressa
L. concentrica
L. concinna
L. consessa
L. consimilis
L. corallorhizae
L. culmorum
L. darkeri
L. defodiens
L. discors
L. dissiliens
L. distributa
L. doliolum
L. drechsleri
L. dryophila
L. ellisiana
L. elongata
L. elymi
L. erigerontis
L. eriophora
L. eumorpha
L. eustoma
L. eustoma forma *leguminosa*
L. eutypoides
L. exocarpogena
L. faulii
L. filamentosa
L. filiformis
L. fimbriata
L. foeniculacea subsp. *lupina*
L. folliculata var. *oxyspora*
L. fraserae
L. fraxini
L. fuckelii
L. fulgida
L. galiorum var. *gnaphaliana*
L. galligena
L. georgius-fischeri
L. halima
L. hamamelidis
L. harknessianna
L. helianthi
L. heliopsidis
L. heloniaefolia
L. hendersoniae
L. hesperia
L. hiemalis
L. houseana
L. hysterioides
L. incarcerata
L. inquinans
L. inspersa
L. interspersa
L. janus
L. kalmiae
L. korrae
L. larseniana
L. lasioderma
L. lassenensis
L. latebrosa
L. leiostega
L. lethalis
L. leucoplaca
L. longipedicellata
L. lophanthi
L. luctuosa
L. lupini
L. lupinicola
L. lyciophila
L. lycopodiicola
L. lycopodina
L. lyndonvillae
L. lythri
L. maclurae
L. major
L. marcyensis
L. marina
L. maydis
L. mellispora
L. mertensiae
L. mesoedema
L. modestula
L. monticola
L. muehlenbergiae
L. muricata
L. muirensis
L. myricae
L. neomaritima
L. nigrans
L. nigricans var. *grindeliae*
L. occidentalis
L. octoseptata
L. odora
L. ogilviensis
L. olericola
L. olivacea
L. olivaespora
L. onagrae
L. opuntiae
L. orae-maris
L. orthogramma
L. pacifica
L. papyricola
L. perplexa
L. phaseolorum

L. phormicola
L. physalidis
L. physostegiae
L. platanicola
L. platypus
L. plurisepta
L. pseudohleria
L. puteana
L. quamoclidii
L. ramulicola
L. rhoina
L. rostrata
L. rubrotincta
L. sabalicola
L. sabaligera
L. sambucina
L. scapophila
L. shastensis
L. sieversiae
L. simmonsii
L. solheimii
L. sorgho-arundinacei
L. sorghophila
L. spartinae
L. sporoboli
L. squamata
L. stereicola
L. sticta
L. stictoides
L. stictostoma
L. straminis
L. subcaespitosa
L. subcompressa
L. subconica
L. subcutanea
L. sublanosa
L. substerilis
L. taxicola
L. tenera
L. tephrosiae
L. tetonensis
L. tini
L. torulispora
L. trimerioides
L. tritici var. *papyricola*
L. tumefaciens
L. typharum
L. utahensis
L. variegata
L. variiseptata
L. veratri
L. virginica
L. viridella
L. wehmeyeri
L. xerophylli
L. zeae
L. zizaniaecola

U.S.S.R.
L. abutilonis
L. aceris
L. aeluropodis
L. agnita var. *bupleuri*
L. alhagii
L. alopecuri
L. ammophile
L. ammothamni
L. amorphae
L. atraphaxidis
L. atriplicis
L. balcarica
L. bataticola
L. batumensis
L. betulina
L. biebersteinii
L. buddlejae
L. calligoni
L. camelliae-japonicae
L. camphorosmae
L. caricis-vulpinae
L. casta
L. cephalariai-uralensis
L. cerei-peruviani
L. chamaeropis
L. chenopodii-albi
L. chochrjakovii
L. clerodendri
L. coniothyrium var. *foliicola*
L. consocians
L. culmorum
L. culmorum forma *epigeii*
L. culmorum forma *phragmitis*
L. culmorum var. *hungarica*
L. daphniphylli
L. davidii
L. dianthi
L. doliolum var. *cacaliae*
L. drabae
L. dubia
L. equiseti
L. feijoae
L. ferruginea
L. ferulicola
L. foliicola
L. frigida
L. ginkgo
L. glandulosae
L. gossypii
L. haloxyli
L. hierochloae
L. holmii
L. hordei
L. hydrangeae
L. hypericola
L. lespedezae
L. lithophilae
L. lonicerae
L. magnoliae
L. media
L. medicaginicola
L. metasequoiae
L. moutan
L. myrti
L. myrticola
L. ornithogali
L. periclymeni var. *tatarica*
L. pleurospora
L. polini
L. pruni
L. pruni var. *plurivora*
L. sanguisorbae
L. scutati
L. secalina
L. sibirica
L. smarodsii
L. sophorae
L. sorbi
L. stipae
L. tanaceti
L. taurica
L. tumefaciens
L. typharum
L. usneae
L. vrieseae
L. weberi
L. woodrow-wilsonii

Uganda
L. hyparrheniae
L. penniseti
L. trichopterygis

Venezuela
L. cryptica
L. espeletiae
L. jahnii
L. orthrosanthi

Yugoslavia
L. altaica
L. andrijevicensis
L. bresadolaeana
L. corrugans
L. fuckelii
L. galiorum subsp. *antirrhini*
L. hesperidicola
L. insulana
L. malyi
L. nicolai
L. pachyasca
L. pachytheca
L. petkovicensis
L. plemeliana
L. rehmiana
L. sclavonica
L. serbica
L. subalpina
L. subsimilis

Zaire
L. canephorae
L. cynodontis-dactyli

Appendix 1. Taxonomic Division of *Leptosphaeria*

P.A. SACCARDO (1883, 1891)

Parasites on dicotyledons.
- Stem/branch inhabiting.
- Leaf inhabiting.
- Fruit and flower inhabiting.

Parasites on monocotyledons.
Parasites on acotyledons.
Species of unknown or doubtful spore color.

F. v. HÖHNEL (1918c)

Scleropleella F. v. Höhnel. Species with typical pseudosphaerialean centra.
Leptosphaeria sensu F. v. Höhnel. Species with typical dothidealean centra.
Nodulosphaeria G.L. Rabenhorst. Species with typical sphaerialean centra.

E. MÜLLER (1950)

Scleropleella. This section, with few exceptions, corresponds to Höhnel's (1918a) generic concept. Generally it includes smaller forms with relatively few egg-shaped or broadly club-shaped asci that are embedded in a more or less well-developed cellular tissue. The ostiole usually is poorly developed.
Eu-Leptosphaeria. This section contains the largest number of species of the four sections. The inner structure corresponds to a higher (more evolved) stage than *Scleropleella*; the asci are more numerous and more slender; the paraphysoids are clearly thread-like, although in some forms a cellular arrangement is still noticeable; the ostiole is conspicuous, and early in development is filled with hyaline cells that only later give way to the pore. Spores are thinner than in *Massariosphaeria*, and are often fusiform, and they have a mucilaginous coat.
Massariosphaeria. This section is composed of forms whose spores (approaching the *Wettsteinina* type) are relatively broad, possess a distinct mucilaginous coat when young, and reach maturity relatively late (at least in part), sometimes only outside the asci. Structure of the fruiting bodies corresponds to that of section *Eu-Leptosphaeria.* These forms may be regarded as transitional to *Massaria.*
Nodulosphaeria. This section is composed of the most highly evolved forms, designated by F. v. Höhnel as "sphaerial." They are distinguished from all others by the ostiole, which is coated with thread-like, periphyses-like hyphae that usually diverge toward the middle of the mouth-channel and toward the "scheitel." In the region of the "scheitel," these periphyses are often replaced by brown bristles. Peridia of fruiting bodies usually consist of several layers of elongate, sometimes almost rectangular cells. The numerous, usually cylindrical-clavate asci are surrounded by thread-like paraphysoids.

A. MUNK (1957)

Eu-Leptosphaeria. Pseudothecia sclerotioid, thickest at the sides. Asci slender, numerous. Ostiole, generally without a periphysoid structure.
Para-Leptosphaeria. Pseudothecia middle-sized, with a uniform, thin peridium; generally no periphysoid structure in the papilla. Interascicular tissue paraphysoid. This section contains a large and heterogenous group of species.
Scleropleella. Pseudothecia small; interascicular tissue obsolete.
Nodulosphaeria. Pseudothecia with a complicated structure of the papilla. It is covered with brown, spiny hairs that extend into the ostiole. Periphysoid tissue is distinct.

L. HOLM (1957)

Leptosphaeria sensu L. Holm. Species similar to the type of the genus *Leptosphaeria doliolum*; they occur principally on dicotyledons.
Nodulosphaeria G.L. Rabenhorst. Species similar to the *Nodulosphaeria* of Müller; they occur on dicotyledons, especially on Compositae.
Phaeosphaeria I. Miyake. Species that correspond essentially to the *Scleropleella* section of Müller (1950) and Munk (1957) and that occur on monocotyledons.

Entodesmium H. Riess. Species with elongated ascospores; they intergrade with *Ophiobolus* and occur on legumes.

R.A. SHOEMAKER (1984)

Leptosphaeria. Circumscribed *Leptosphaeria* in a broad concept of Holm and Müller; however, many segregate genera were accepted. The genus always lacks erect setae on ascomata. The walls of the ascocarps often have scleroplectenchyma at least near the beak base. The physes are broad, septate with or without guttules and cytoplasmic accumulations and frequently with an external gelatinous coating. Asci are biseriate or, rarely, uniseriate. Ascospores are fusiform, cylindric or clavate, 3-septate or more, and the first formed septum is constricted and near the middle. These ascospores frequently have globose, terminal appendages that are rarely entirely sheathed. No woody parts of dicotyledonous plants are the usual susbstrates.

M.E. BARR (1987a, 1987b)

Leptosphaeriaceae. Established the family Leptosphaeriaceae based on *Leptosphaeria*, but also included *Curreya*, *Didymolepta*, *Heptameria*, and *Ophiobolus*. The family was segregated from the Pleosporaceae because of the coelomycetous rather than the hyphomycetous anamorphs and because of the narrow, thin-walled asci. It differs from the Phaeosphaeriaceae in having conoid and applanate or obpyriform or sphaeroid ascomata, whose walls are scleroplectenchymatic.

Appendix 2. Genera Historically Allied to *Leptosphaeria*

Bricookea M.E. Barr, Mycotaxon. An International Journal Designed to Expedite Publication of Research on Taxonomy & Nomenclature of Fungi & Lichens, Ithaca, New York 15:346. 1982. Type species: *Bricookea sepalorium* (J.S. Vleugel) M.E. Barr. Family: Phaeosphaeriaceae. Ascomata: Clustered, immersed, subepidermal, separate or as locules in crustose stromatic tissues, globose, radiate arrangement of cells of peridium. Asci: Bitunicate, oblong, short-stalked, numerous, basal. Ascospores: Fusiform to narrowly obovoid, 3-septate, hyaline. Anamorph: Unknown. Remarks: Barr (1982) erected this genus for a species of *Leptosphaeria* described from inflorescences of *Juncus* and considers it to be related to *Phaeosphaeria*.

Chaetomastia (P.A. Saccardo) A.N. Berlese, Icones Fungorum Omnium Hucusque Cognitorum ad usum Sylloges Saccardianae Adcommodatae 1:38. 1891. Lectotype species: *Chaetomastia hirtula* (P.A. Karsten) A.N. Berlese. Family: Dacampiaceae. Ascomata: Immersed-subepidermal, becoming erumpent, scattered or clustered, obpyriform or ovoid to globose; apex wide, blunt, ostiole rounded or slit-like; wall pseudoparenchymatous, cells externally darkened and thickened in upper regions. Asci: Bitunicate, clavate or cylindric, 4-, 6-, or 8-spored. Ascospores: Biseriate or uniseriate; obovoid elongate, 3- to 11-septate; cell above first septum enlarged; wall wide, dark, smooth or verruculose; yellowish brown becoming dark brown or reddish brown. Anamorph: Coelomycetous where known; conidia hyaline or brown, 1- to 2-celled (*Aposphaeria*-like or *Coniothyrium*-like). Remarks: This genus is distinguished by the obpyriform or obovoid ascomata with a wide apical papilla, peridium of small dark cells that is widest and 3-layered in the upper region, and by dark asymmetric phragmospores (Barr 1989).

Chaetoplea (P.A. Saccardo) F.E. Clements, *in* F.E. Clements and C.L. Shear, The Genera of Fungi, pp. 74, 275. 1931. ≡*Pyrenophora* subgen. *Chaetoplea* P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:279. 1883. Type species: *Chaetoplea calvescens* (E.M. Fries ex J. Desmazières) F.E. Clements & C.L. Shear. ≡*Sphaeria calvescens* E.M. Fries, Scleromyceti Sueciae. Collegit, Digessit et Evulgaviti, No. 401. Unpublished? ≡*Pyrenophora calvescens* (E.M. Fries ex J. Desmazières) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:279. 1883. Family: Phaeosphaeriaceae. Ascomata: Seated on a subiculum, globose or depressed globose, dark brown to black, subepidermal becoming superficial, wall composed of polygonal cells, surrounded by stiff dark hyphae. Asci: Bitunicate, numerous, cylindrical, short-stalked with thickened apical walls, 8-spored. Ascospores: Fusoid-ellipsoid, straight or inequilateral with three transverse septa and with longitudinal septa, yellowish brown or dark brown, smooth or finely verruculose. Remarks: This genus has only recently been accepted by Barr (1981, 1987b), who placed it in the Phaeosphaeriaceae. The type species, *Chaetoplea calvescens*, has been placed in *Pleospora* by Webster and Lucas (1959), Wehmeyer (1961), and Shoemaker (1968). Crivelli (1983) transferred *Chaetoplea calvescens* to *Leptosphaeria*, and Eriksson and Hawksworth (1986) synonymized *Chaetoplea* with *Leptosphaeria*.

Curreya P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:651. 1883. Type species: *Curreya conorum* (L. Fuckel) P.A. Saccardo. Family: Leptosphaeriaceae. Ascomata: Scattered, immersed-subepidermal, depressed globose; wall scleroplectenchymatic, melanized black, surface of textura angularis; beak absent. Asci: Many, bitunicate, cylindrical-clavate, thick-walled in apical region, short-stalked, containing eight ascospores. Ascospores: Obovate, constricted at septa, slightly asymmetrical, with one or more enlarged cells, 7-septate or more, with longitudinal septa, most cells smooth-walled, surrounded by a gel layer.

Remarks: The genus is included in the Leptosphaeriaceae by Barr (1987b) and differs from *Leptosphaeria* in having longitudinally septate ascospores.

Didymolepta A. Munk, Dansk Botanisk Arkiv, Kjøbenhavn 15(2):110. 1953. Type species: *Didymolepta winteriana* (P.A. Saccardo) A. Munk. Family: Leptosphaeriaceae. Ascomata: Scattered, conic, glabrous, black; wall of scleroplectenchymatic cells melanized black; beak absent. Asci: Bitunicate, subcylindric, sessile, thick-walled, with eight ascospores. Ascospores: 1-septate, hyaline. Anamorph: Unknown. Remarks: This genus has been placed in the Leptosphaeriaceae by Barr (1987b), and it differs from other genera in the family by having 1-septate ascospores.

Entodesmium H. Riess, Hedwigia, Dresden 1:28. 1854. Type species: *Entodesmium rude* H. Riess. Family: Phaeosphaeriaceae? Ascomata: Scattered or clustered, more or less lageniform, slightly hairy; beaks very long. Asci: Many, bitunicate, cylindric to narrowly clavate, short-stalked. Ascospores: Cylindrical, 4-septate or more, with a clearly delimited apical portion and bipolar appendages. Anamorph: Unknown. Remarks: This genus was recognized by Holm (1957) for a small group of *Leptosphaeria* species found on Leguminosae.

Graphyllium F.E. Clements, Studies in the Vegetation of the State. Nebraska University. Botanical Survey. Report on Recent Collections, Lincoln 5:6. 1901. Type species: *Graphyllium chloes* F.E. Clements. Family: Phaeosphaeriaceae. Ascomata: Flattened-globose, finally collapsing-pezizoid, with more or less dark brown, radiating hyphal tomentum about the base. Asci: Bitunicate, stout-clavate, thick-walled. Ascospores: Strongly flattened in one plane, fusoid-ellipsoid to clavate-ellipsoid, with a single vertical septum running through the central cells but not through the end cells in face view, yellow-brown to dark red-brown. Anamorph: Unknown. Remarks: *Graphyllium* is the earliest name for species formally placed in *Platyspora* L.E. Wehmeyer and *Comoclathris* F.E. Clements (Barr 1987b).

Heptameria H. Rehm & F. v. Thümen, Instituto. Revista Scientifica e Litteraria, Coimbra, Series 2, 27:252. 1879. Type species: *Heptameria elegans* H. Rehm & F. v. Thümen. Family: Leptosphaeriaceae. Ascomata: Clustered, immersed-subepidermal, becoming erumpent, subglobose to conical, rough-surfaced, black, short papillate. Asci: Bitunicate, clavate, short-stalked, with eight ascospores. Ascospores: Fusiform, 7-septate or more, with dark central portion having longitudinal septa, brown. Anamorph: Pycnidial with hyaline, oblong, 1-celled conidia. Remarks: This genus was included in the Leptosphaeriaceae by Barr (1987b), and it differs from *Leptosphaeria* by having ascospores with longitudinal septa in the enlarged central cells. Jaczewski (1894) considered that *Heptameria* could be interpreted as a section of *Leptosphaeria*, but the study of Lucas and Sutton (1971) indicates that the genus is distinct.

Herpotrichia L. Fuckel, Fungi Rhenani Exsiccati A Leopoldo Fuckel Collecti, Fascicle 22, No. 2771. Anno 1868. Type species: *Herpotrichia rubi* L. Fuckel. Family: Lophiostomataceae. Ascomata: Globose to conic, immersed, becoming erumpent, or superficial on a subiculum, tomentose. Asci: Bitunicate, cylindrical to clavate. Ascospores: Fusiform to ellipsoidal, 1- to 3-septate, hyaline to dull or dark brown, usually with gel coating elongated beyond spore apices. Anamorph: *Coelomycetous*, *Pyrenochaeta*, or *Phoma*-like. Remarks: Differs from *Leptosphaeria* in the tomentose ascocarps on a subiculum and ascospores that can be 1-septate.

Kalmusia G. Niessl v. Mayendorf, Verhandlungen des Naturforschenden Vereins in Brünn 10:204. 1872. Type species: *Kalmusia ebuli* G. Niessl v. Mayendorf. Family: Phaeosphaeriaceae. Ascomata: Subglobose, immersed in an effuse stroma. Asci: Bitunicate, clavate, long stipitate. Ascospores: Oblong, curved, 3-septate, brown. Anamorph: Unknown. Remarks: This genus differs from *Leptosphaeria* in having a stroma and long, stipitate asci.

Keissleriella F. v. Höhnel, Sitzungsberichte der Akademie der Wissenschaften in Wien. Mathematisch-naturwissenschaftliche Klasse. Abt. I, 128:582. 1919. Type species: *Keissleriella aesculi* (F. v. Höhnel) F. v. Höhnel. Family: Melannomataceae. Anamorphs: *Ascochyta* M.A. Libert and *Dendrophoma* P.A. Saccardo. Remarks: Holm (1957) accepted the genus *Trichometasphaeria* A. Munk but stated that there may be earlier generic names for those Ascomycetes with setose pseudothecia placed in the Massarinaceae by Munk (1956), for example, *Keissleriella* F. v. Höhnel. This later genus differed in having 1-septate ascospores vs. several septate in *Trichometasphaeria*. Bose (1961) united the two genera under the earlier name *Keissleriella* after observing variation in ascospore septation in *Keissleriella aesculi*.

Lidophia J. Walker & B.C. Sutton, Transactions of the British Mycological Society, London 62:232. 1974. Type species: *Lidophia*

graminis (P.A. Saccardo) J. Walker & B.C. Sutton. =*Dilophia* P.A. Saccardo, 1883, non *Dilophia* T. Thomas, 1953 (Cruciferae). Family: Leptosphaeriaceae. Ascomata: Embedded in a stroma, spherical. Asci: Bitunicate, cylindrical, apically thickened. Ascospores: Narrowly fusiform, widest at the middle and tapering gradually into an elongated fine thread at each end, ~15-septate, yellow, breaking into equal spore parts at maturity. Anamorph: Unknown, but *Dilophospora* is found in same stroma. Remarks: The ascospores of *Lidophia* were considered indistinct from those of *Leptosphaeria* (Müller 1950; v. Arx and Müller 1975); however, Walker (1980) considers *Lidophia* distinct from *Leptosphaeria* and close to *Ophiobolus* in that the ascospores readily break into half-spores at the central septum. *Lidophia* differs from *Ophiobolus* in lacking an enlarged central cell in the ascospore.

Lophiostoma V. Cesati & G. de Notaris, nom. cons., Commentario della Società Crittogamologica Italiana, Milan 1:219. 1863. Type species: *Lophiostoma macrostoma* (H.J. Tode:E.M. Fries) V. Cesati & G. de Notaris. Based on *Sphaeria macrostoma* H.J. Tode:E.M. Fries. Family: Lophiostomataceae. Ascomata: Immersed, subepidermal, globose to subglobose, glabrous, cells of outer wall melanized black, beak laterally compressed, clypeate. Asci: Bitunicate, many, cylindro-clavate, wall thin but thick at apex, short-stalked, eight-spored. Ascospores: Obliquely uniseriate, ellipsoidal to narrowly clavate, brown, 3- to 7-phragmoseptate, 1 to 2 longitudinal septa present. Anamorph: Unnamed pycnidial anamorph (Chesters and Bell 1970). Remarks: *Lophiostoma* differs from *Leptosphaeria* in having ascomata, with laterally compressed papillae (Chesters and Bell 1970).

Massaria G. de Notaris, Nuovo Giornale Botanico Italiano e Bolletino della Società Botanica Italiana, Firenze 1:333. 1844. Type species: *Massaria inquinans* (H.J. Tode:E.M. Fries) G. de Notaris. Basionym: *Sphaeria inquinans* H.J. Tode:E.M. Fries. Family: Massariaceae. Ascomata: Immersed in pseudostromatic tissue or a clypeus becoming erumpent or superficial with bases remaining immersed. Asci: Bitunicate, subcylindrical with a short, stout stipe, ocular region low and broad surrounded by a refractive ring. Ascospores: Large, distoseptate, and 3-septate. Anamorph: None reported (Müller 1979). Remarks: The ascospores of *Massaria* are generally larger than in *Leptosphaeria*. Each ascus has an apical cytoplasmic protrusion surrounded by a refractive ring and usually four ascospores at maturity. The ascospores are larger than those in *Leptosphaeria* and have a thick epispore and a mucilaginous coat (Barr 1979).

Massarina P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:153. 1883. Lectotype species: *Massarina eburnea* (L.R. Tulasne & C. Tulasne) P.A. Saccardo. Family: Lophiostomataceae. Ascomata: Clustered, immersed, subepidermal, depressed, glabrous, cells of outer ascocarp wall melanized brown, wall tissue of textura prismatica in face view, beak absent, ostiole circular. Asci: Many, bitunicate, cylindric to cylindric-clavate, short-stalked, wall thick at apex. Ascospores: Biseriate, oblong-fusoid, 3-septate, slightly constricted at the septa, symmetrical, hyaline to subhyaline, frequently surrounded by a mucous sheath, which may be evanescent. Anamorphs: *Anguillospora* C.T. Ingold, *Ceratophoma* F. v. Höhnel, *Coniothyrium* A.C. Corda, *Diplodia* E.M. Fries, *Microsphaeropsis* F. v. Höhnel, and *Stagonospora* P.A. Saccardo. Remarks: *Massarina* is allied with *Leptosphaeria* species having hyaline ascospores (*Metasphaeria* sensu P.A. Saccardo, 1883) but differs in formation of a clypeus and in the ascospores, which form their secondary septa late in development (Munk 1956; Bose 1961; Müller 1979).

Massariosphaeria (E. Müller) P.G. Crivelli, Dissertation Eigenössischen Technischen Hochschule, Zürich, No. 7318:141. 1983. Type species: *Massariosphaeria phaeospora* (E. Müller) P.G. Crivelli. Family: Dacampiaceae. Ascomata: Scattered, globose to conic, immersed, subcuticular to subepidermal, becoming erumpent, beak papillate, conical to longitudinally compressed with a circular or slit-like ostiole. Asci: Bitunicate, numerous, clavate-cylindrical, short-stalked, thick-walled. Ascospores: Phragmoseptate, sometimes with longitudinal septa, hyaline to brown, fusiform to ellipsoid or clavate. Anamorph: *Aposphaeria*-like, *Phoma*-like. Remarks: Müller (1950) segregated species of *Leptosphaeria* with large, thick-walled ascospores with thick gelatinous sheaths into the subgenus *Massariosphaeria*. Crivelli (1983) elevated the subgenus to genus and expanded it to include dictyosporous species. It appears to be a natural grouping with easily distinguished features.

Melanomma T. Nitschke ex L. Fuckel, Symbolae Mycologicae, p. 159. 1870. Lectotype species: *Melanomma pulvis-pyris* (C.H.

Persoon:E.M. Fries) L. Fuckel. Family: Melanommataceae. Anamorphs: *Aposphaeria* P.A. Saccardo and *Pseudospiropes* M.B. Ellis. Remarks: Holm (1957) maintained *Melanomma* for certain lignicolous species that appear to form a unit based on the scleroplectenchymatic walls of the ascocarps. The ascospores are 3-septate, ellipsoidal or frequently cuneiform to nearly clavate and uniformly brown. *Melanomma* was further subdivided into four groups based on variability and differentiation of the ascocarp wall. A number of species on dead herbaceous stems usually placed in *Leptosphaeria* were transferred to *Melanomma*. Holm (1957) considered *Melanomma* to be closely related to *Leptosphaeria*, but Samuels and Müller (1978) believed that *Melanomma* should be merged with *Trematosphaeria* (Chesters 1938).

Montagnula A.N. Berlese, Icones Fungorum Omnium Hucusque Cognitorum ad usum Sylloges Saccardianae Adcommodatae 2:68. 1896. Type species: *Montagnula infernalis* (G. Niessl v. Mayendorf) P.G. Crivelli. Family: Phaeosphaeriaceae. Ascomata: With or without a clypeus or surrounded by a secondary stromatic development, globose. Asci: Bitunicate, clavate, with filiform basal stalk having a claw-like base, wall thickened. Ascospores: Fusoid, mostly 3-, rarely 4-, 5-, or 7-septate, dark red-brown to opaque, wall often finely tuberculate, vertical walls in two central cells, symmetric, constricted at the central septum. Anamorph: Unknown. Remarks: Considered a subgenus of *Pleospora* by Wehmeyer (1961), *Montagnula* was raised to generic rank by Crivelli (1983). Characteristics distinguishing the group are the tapered or elongate stipitate base of the ascus, the usually very dark pigmentation of the spore wall (which is often tuberculate-roughened), the tardy insertion of vulgaris-like septa in the central cells, the tendency to form a thick ascostromatic wall, and a surrounding clypeus or stroma.

Nodulosphaeria G.L. Rabenhorst, Klotzschii Herbarium Vivum Mycologicum Sistens Fungorum Per Totam Germaniam Cresentium Collectionem Perfectam, Dresden, Edition II, Century 8, No. 725. Anno. 1858. Type species: *Nodulosphaeria derasa* (M.J. Berkeley & C.E. Broome) L. Holm. Family: Phaeosphaeriaceae. Ascomata: Clustered, immersed-subepidermal, globose, setose, wall pseudoparenchymatic, melanized brown, of textura angularis, beak short, with paraphyses. Asci: Many, bitunicate, cylindro-clavate, short-stalked, containing eight ascospores. Ascospores: Fusiform, constricted at mid-septum, 8- to 10-septate, with one enlarged cell, with bipolar appendages, pale brownish yellow. Anamorph: Unknown. Remarks: Once considered a subgenus of *Leptosphaeria*, *Nodulosphaeria* was reinstated by Holm (1957). This genus can be distinguished from *Leptosphaeria* by the setose ascomata composed of pseudoparenchyma.

Ophiobolus H. Riess, Hedwigia, Dresden 1:27–28. 1854. Type species: *Ophiobolus disseminans* H. Riess. Family: Leptosphaeriaceae. Ascomata: Scattered to clustered, immersed, becoming erumpent, pyriform, black, glabrous, outer wall of textura globulosa melanized brown, inner wall of textura prismatica, wall pseudoparenchymatic. Asci: Bitunicate, numerous, long-cylindrical to clavate, thick-walled at tips, short-stalked, 4- to 8-spored. Ascospores: In a single fascicle, yellow or brown, sclolecosporous, multiseptate, often with one or more enlarged cells, sometimes with one or more gelatinous, terminal, globose appendages. Anamorph: Unknown. Remarks: *Ophiobolus* integrates with *Leptosphaeria* subgenus or section *Nodulosphaeria* (G.L. Rabenhorst sensu F. v. Höhnel) E. Müller, and authors do not agree on the precise limit between *Ophiobolus* and subgenus *Nodulosphaeria*. In general, the ascospores of subgenus *Nodulosphaeria* are only slightly curved or straight and shorter than those in *Ophiobolus*, and dark periphyses line the ostiole in subgenus *Nodulosphaeria* (Shoemaker 1976, Walker 1980).

Ophiosphaerella C.L. Spegazzini, Anales del Museo Nacional de Historia Natural de Buenos Aires 19(Series 3, 12):401. 1909. Type species: *Ophiosphaerella graminicola* C.L. Spegazzini. Family: Phaeosphaeriaceae. Ascomata: Scattered to clustered, immersed, subepidermal, globose, glabrous, wall of textura angularis in face view, beak short, papillate, bluntly conical with periphyses. Asci: Bitunicate, long, cylindric, in a dense basal layer. Ascospores: Filiform (scolecosporous), phragmoseptate, brown, lacking gelatinous sheaths. Anamorph: Unknown. Remarks: A genus close to *Ophiobolus* H. Riess *sensu stricto* and *Phaeosphaeria* I. Miyake, it is characterized by scolecosporous, brown, septate ascospores and occurs on Gramineae and Cyperaceae.

Paraphaeosphaeria O. Eriksson, Arkiv för Botanik, Uppsala, Stockholm, Series 2, 6:405. 1967. Type species: *Paraphaeosphaeria michotii* (G.D. Westendorp) O. Eriksson. Family: Phaeosphaeriaceae. Ascomata: Scattered, intraepidermal, depressed globose to globose, without prominent beak. Asci: Bitunicate,

numerous, cylindrical, short-stalked. Ascospores: Clavate to cylindrical, 2- to 9-septate, first-formed septum subtending an enlarged cell, echinulate to rarely smooth, with a thick, gelatinous sheath. Anamorph: *Coniothyrium* A.C.J. Corda. Remarks: *Paraphaeosphaeria* is a segregate of *Leptosphaeria* resembling *Phaeosphaeria*, but differs in having ascospores with more septa and *Coniothyrium* anamorphs. In *Phaeosphaeria*, the anamorphs belong to *Hendersonia* P.A. Saccardo and *Phaeoseptoria* C.L. Spegazzini (Eriksson 1967).

Phaeosphaeria I. Miyake, Botanical Magazine, Tokyo 23:93. 1909; Journal of the College of Agriculture, Imperial University of Tokyo 2:246. 1910. Type species: *Phaeosphaeria oryzae* I. Miyake. Family: Phaeosphaeriaceae. Ascomata: Superficial, globose, glabrous, wall pseudoparenchymatic, thin. Asci: Many, bitunicate, cylindro-clavate, containing eight ascospores. Ascospores: Fusiform to cylindrical, 3-septate, yellowish brown, one cell clearly inflated. Anamorph: Coelomycetous, *Phyllosticta*/*Hendersonia*. Remarks: Ascospores of species in this genus are very similar to those of *Leptosphaeria* species. *Phaeosphaeria* species are distinguished by small thin-walled, pseudoparenchymatic ascomata, and by their occurrence mostly on monocots (Shoemaker and Babcock 1989).

Platystoma V. Trevisan, Bulletin. Société R. de Botanique de Belgique, Bruxelles 16:16. 1877. Type species: *Platystoma compressum* (C.H. Persoon:E.M. Fries) V. Trevisan. ≡*Sphaeria compressa* C.H. Persoon:E.M. Fries. Family: Platystomaceae. Ascomata: Clustered, immersed-subepidermal, globose, glabrous, outer cells melanized brown, short papillate, papilla conical with periphyses, ostiole slit-like. Asci: Many, bitunicate, cylindric-clavate, short-stalked. Ascospores: Fusiform to subcylindric, constricted at septa, 5- to 6-septate, with one enlarged cell, brown. Anamorph: Unknown. Remarks: This genus differs from *Leptosphaeria* in having trabeculate rather than cellular pseudoparaphyses and a slit-like ostiole.

Pleospora G.L. Rabenhorst ex V. Cesati & G. de Notaris, nom. cons., Commentario della Società Crittogamologica Italiana, Milan 1:217. 1863. Type species: *Pleospora herbarum* (C.H. Persoon:E.M. Fries) G.L. Rabenhorst type cons. Family: Pleosporaceae. Ascomata: Perithecioid, immersed-erumpent, peridium relatively wide, composed of pseudoparenchyma. Asci: Bitunicate, clavate or oblong, short-stalked, endotunica wide. Ascospores: Elliptical, yellow-brown, with transverse and longitudinal septa, with gelatinous sheath. Anamorphs: *Alternaria* C.G. Nees v. Esenbeck, *Dendryphion* K.F.W. Wallroth, and *Stemphylium* K.F.W. Wallroth. Remarks: *Pleospora* can be separated from *Leptosphaeria* by ascospore septation and anamorphs. Some species included in *Leptosphaeria* have ascospores with longitudinal septa, and these species must be examined carefully for ascomatal features and cultured for anamorphic states (Müller 1951, Wehmeyer 1961).

Pyrenophora E.M. Fries, Summa Vegetabilium Scandinaviae, Seu Enumeratio, Systematica et Critica, Plantarum tum Cotyledonearum, Quam Nemearum Inter Mare Occidentale Et Album, Inter Eidoram et Nordkop, Hactenus Lectorum, una Cum Singulae Distributione Geographica, pp. 397–398. 1849. Type species: *Pyrenophora phaeocomes* (G.L. Rabenhorst:E.M. Fries) E.M. Fries. Family: Pyrenophoraceae. Ascomata: Immersed to erumpent, medium to large, usually setose or bearing conidiophores. Asci: Bitunicate, few, basal, clavate, oblong or cylindric. Ascospores: Ellipsoidal, broader above the middle, muriform, yellowish-brown, sheathed. Anamorph: *Drechslera* R.A. Shoemaker. Remarks: *Pyrenophora* is closely related to *Pleospora* and differs from *Leptosphaeria* in having large, muriform ascospores with gelatinous sheaths. The genus is nomenclaturally sound with the conservation of *Ceuthospora* R.K. Greville, 1826, typified by *Ceuthospora lauri* (R.K. Greville) R.K. Greville vs. *Ceuthospora* E.M. Fries, 1825, typified by *Ceuthospora phaeocomes* (J.F. Rebentish:E.M. Fries) E.M. Fries (Shoemaker 1961, Ammon 1963, Barr 1972, Sutton 1972).

Rebentischia P.A. Karsten, Fungi Fenniae Exsiccati, Century 9, No. 881. Anno. 1869; Mycologia Fennica, p. 14. 1873. Type species: *Rebentischia pomiformis* P.A. Karsten. Family: Tubeufiaceae. Ascomata: Erumpent, globose, roughened with protruding cells and hyphae, pseudoparenchymatic, outer cells melanized black, beak absent. Asci: Many, bitunicate, cylindric-clavate. Ascospores: Obovate, vinaceous brown 4- to 5-septate, with basal appendage. Anamorph: Unknown. Remarks: Müller (1950) considered the centrum type of this genus to be similar to that of a typical *Leptosphaeria*. It differs from *Leptosphaeria* in the ascospores, which have a hyaline basal appendage (Dennis 1978, Barr 1980).

Sulcispora R.A. Shoemaker, Canadian Journal of Botany, Ottawa 67:1594. 1989. Type

species: *Sulcispora pleurospora* (G. Niessl v. Mayendorf) R.A. Shoemaker. Family: Phaeosphaeriaceae. Ascomata: Immersed becoming erumpent, pyriform to globose, smooth. Beak: Composed of brown rectangular cells, the ostiole lacking periphyses. Ascoma wall: Brown pseudoparenchymatic, rectangular cells. Asci: Few, bitunicate, cylindric, 8-spored. Ascospores: Tetraseriate, fusiform, straight, 5- to 6-septate, constricted at first septum, reddish-brown, longitudinally sulcate, sheathed.

Trematosphaeria L. Fuckel, Symbolae Mycologicae, pp. 161–162. 1870. Type species: *Trematosphaeria pertusa* (C.H. Persoon: E.M. Fries) L. Fuckel. Family: Platystomaceae. Ascomata: Superficial to partially immersed, globose to conic, peridium pseudoparenchymatic, melanized black, textura angularis in face view, beak short, papillate. Asci: Bitunicate, cylindric-clavate, short-stalked, containing eight ascospores. Ascospores: Fusiform, constricted at mid-septum, 3-septate, brown. Anamorph: Unknown. Remarks: Petrak (1923) considered the structural features of *Trematosphaeria* to correspond to those of *Leptosphaeria*, and he included wood-inhabiting *Leptosphaeria*-like species. Boise (1984) redefined the genus by the presence of trabeculate pseudoparaphyses and included it in the Platystomaceae in the Melanommatales.

Trichometasphaeria A. Munk, Dansk Botanisk Arkiv, Kjøbenhavn 15(2):135. 1953. Type species: *Trichometasphaeria dianthi* (E. Rostrup) A. Munk. [=*Trichometasphaeria gloeospora* (M.J. Berkeley & F. Currey) L. Holm]. Family: Lophiostomataceae. Ascomata: Globose, subepidermal, with ostiole bearing brown setae. Asci: Bitunicate, clavate to cylindrical. Ascospores: Hyaline, fusiform to elliptical, 4- to 6-septate. Anamorph: Unknown. Remarks: This genus is similar to *Keissleriella*, but it differs in having several septate spores versus 1-septate spores in *Keissleriella*. Bose (1961) united the two genera under the earlier name, *Keissleriella*, after observing variation in ascospore septation in *Keissleriella aesculi*. Barr (1987b) accepts both genera and places each of them in a different order.

Appendix 3. Synonyms of *Leptosphaeria*

Ampullina L. Quélet (1875). Type: *Ampullina acuta* =*Leptosphaeria acuta* (v. Arx and Müller 1975).

Baumiella P.C. Hennings *in* H. Baum (1903). Type species: *Baumiella caespitosa* P. Hennings *in* H. Baum, Kunene-Sambesi Expedition, Berlin, p. 165. 1903; ≡*Leptosphaeria baumii* J.A. v. Arx & E. Müller (1975) nom. nov., non *Leptosphaeria caespitosa* G. Niessl v. Mayendorf.

Bilimbiospora B. Auerswald *in* G.L. Rabenhorst (1860). Nomina generica rejicienda by conservation of *Leptosphaeria* (Greuter et al. 1988).

Chaetoplea (P.A. Saccardo) F.E. Clements *in* F.E. Clements & C.L. Shear (1931). =*Leptosphaeria* (Eriksson & Hawksworth 1986).

Chitonospora E.C. Bommer, M.H. Rousseau, & P.A. Saccardo *in* P.A. Saccardo (1891). =*Leptosphaeria* (Müller 1950).

Dendroleptosphaeria M. de Sousa da Camara (1932). A possible synonym of *Leptosphaeria* (Eriksson & Hawksworth 1986).

Dothideopsella F. v. Höhnel (1915). =*Leptosphaeria* (v. Arx & Müller 1975).

Exilispora L.R. Tehon & E.Y. Daniels (1927). Type species: *Exilispora plurisepta* L.R. Tehon & E.Y. Daniels, Mycologia, Lancaster, Pennsylvania 19:112. 1927; =*Leptosphaeria plurisepta* (L.R. Tehon & E.Y. Daniels) J.A. v. Arx & E. Müller (v. Arx & Müller 1975).

Humboldtina C.E. Chardon & R.A. Toro (1934). =*Leptosphaeria* (Eriksson & Hawksworth 1986).

Leptosporopsis F. v. Höhnel (1920). =*Leptosphaeria* (Eriksson & Hawksworth 1986).

Macrobasis K. Starbäck (1893). =*Leptosphaeria* (Petrak and Sydow 1923, Müller 1950).

Metasphaeria P.A. Saccardo (1883). Nomen ambiguum. =*Leptosphaeria* (Dothideales) (v. Arx and Müller 1975); a segregate of *Leptosphaeria* comprising the hyaline-spored species, otherwise as in *Leptosphaeria* (Petrak 1923, Müller 1950). However, the genus contains both unitunicate and bitunicate Ascomycetes (Barr 1976).

Mycopyrenula E.A. Vainio (1921). =*Leptosphaeria* (Müller 1950), but considered a good genus by Hawksworth et al. (1983).

Mycotodea W. Kirschstein (1936). According to Petrak (1940), *Mycotodea* is a synonym of *Scleropleella* and thus *Leptosphaeria* according to E. Müller (1950); =*Leptosphaeria* (Dothideales) (v. Arx and Müller 1975).

Myriocarpium H.F. Bonorden (1864). =*Leptosphaeria* (Eriksson & Hawksworth 1986).

Nodulosphaeria G.L. Rabenhorst (1858). Nomina generica rejicienda by the conservation of *Leptosphaeria* (Grueter 1988).

Phaeoderris (P.A. Saccardo) F. v. Höhnel (1907b). =*Leptosphaeria* (v. Arx and Müller 1975).

Phyllophthalmaria (J. Muller Argov) A. Zahlbruckner *in* A. Engler & K. Prantl (1905). A questionable synonym of *Leptosphaeria* (Eriksson and Hawksworth 1986).

Pocosphaeria (P.A. Saccardo) A.N. Berlese (1892). =*Leptosphaeria* (Müller 1950, v. Arx and Müller 1975). Represents *Leptosphaeria* species with a bristly peridium.

Saccothecium E.M. Fries (1835). =*Pringsheimia* S. Schulzer v. Müggenburg *in* S. Schulzer v. Müggenburg, A. Kanitz, and J.A. Knapp (1866). Placed in the Dothideales (Holm 1975); =*Massaria* G. de Notaris (1844) (Pyrenulales) (Barr 1979).

Sclerodothis F. v. Höhnel (1918a). Based on hyaline spores and therefore identical with *Metasphaeria*, which is a synonym of *Leptosphaeria* (v. Arx & Müller 1975).

Scleropleella F. v. Höhnel (1918a). =*Leptosphaerulina* D. McAlpine (1902) (Dothideales) (Barr 1972); considered a good section or subgenus of *Leptosphaeria* by Müller (1950); species in this group form transitional taxa within *Leptosphaeria*.

Syncarpella F. v. Theissen & H. Sydow (1915). =*Leptosphaeria* (v. Arx and Müller 1975). Accepted by Barr 1987b.

Appendix 4. Anamorphs of *Leptosphaeria*

Ascochyta M.A. Libert (Coelomycete). Connection: *Leptosphaeria pratensis* P.A. Saccardo & P.A. Briard [=*Ascochyta meliloti* (W. Trelease) J.J. Davis]. Source: Kendrick and DiCosmo 1979. Conidiogenesis: Phialidic with periclinal thickenings of apex of phialide. Conidia: Hyaline, 1- or, rarely, 3-septate. Comments: Other anamorphs reported for *Leptosphaeria pratensis* P.A. Saccardo & P.A. Briard are *Phoma meliloti* A. Allescher and *Stagonospora meliloti* (W.G. Lasch) F. Petrak, both Coelomycetes (Lucas and Webster 1967).

Ascochytula (A.A. Potebnia) H. Diedicke [=*Pseudodiplodia* (P.A. Karsten) P.A. Saccardo] (Coelomycete). Connection: *Leptosphaeria obiones* (H.M. Crouan & P.L. Crouan) P.A. Saccardo (=*Ascochytula obiones* H. Diedicke). Source: Grove 1935 (by association). Conidiogenesis: Phialidic with periclinal thickening of apex of phialide. Conidia: Phaeodidymospores.

Asteromella G. Passerini & F. v. Thümen (Coelomycete). Connection: *Leptosphaeria artemisiae* (L. Fuckel) B. Auerswald (=*Asteromella artemisiae* E. Müller). Source: Müller 1950, Lucas and Webster 1967. Conidiogenesis: Phialidic with periclinal thickening of apex of phialide. Conidia: Hyaloamerospores.

Camarosporium S. Schulzer v. Müggenburg (Coelomycete). Connection: *Leptosphaeria maculans* (J. Desmazières) V. Cesati & G. de Notaris [=*Camarosporium affine* (P.A. Saccardo) E.C. Bommer & M.H. Rousseau] (Coelomycete). Source: Müller and Tomaševič 1957; Connection: *Leptosphaeria millefolii* (L. Fuckel) G. Niessl v. Mayendorf (=*Camarosporium* sp.). Source: Müller and Tomaševič 1957; Connection: *Leptosphaeria ogilviensis* (M.J. Berkeley & C.E. Broome) V. Cesati & G. de Notaris (=*Camarosporium* sp.). Source: Müller and Tomaševič 1957; Connection: *Leptosphaeria orthosanthi* E. Müller (=*Camarosporium* sp.). Source: Müller and Dennis 1965; Conidiogenesis: Annellidic. Conidia: Phaeodictyospores.

Cladosporium J.H. Link (Hyphomycete). Connection: *Leptosphaeria ladina* E. Müller (=*Cladosporium ladium* E. Müller). Source: Müller 1950. Conidiogenesis: Holoblastic, sympodial. Conidia: Brown, o-pluriseptate. Comments: Considered a culture contaminant rather than an anamorph (Kendrick and DiCosmo 1979).

Coniothyrium (A.C.J. Corda) (Coelomycete). Connection: *Leptosphaeria bondari* A.A. Bitancourt & A.E. Jenkins (=*Coniothyrium* sp.). Source: Wehmeyer 1975; Connection: *Leptosphaeria coniothyrium* (L. Fuckel) P.A. Saccardo (=*Coniothyrium fuckelii* P.A. Saccardo). Source: Zeller 1927, Punithalingam 1980; Connection: *Leptosphaeria faullii* G.D. Darker (=*Coniothyrium faullii* G.D. Darker). Source: Darker 1964, Wehmeyer 1975; Connection: *Leptosphaeria michotii* (G.D. Westendorp) P.A. Saccardo (=*Paraphaeosphaeria* O. Eriksson; =*Coniothyrium scirpi* J.W. Trail). Source: Wehmeyer 1975; Sivanesan 1984; Connection: *Leptosphaeria obiones* (H.M. Crouan & P.L. Crouan) P.A. Saccardo (=*Coniothyrium obiones* H. Diedicke). Source: Grove 1935; Connection: *Leptosphaeria perichymeni* C.A. Oudemans (=*Coniothyrium* sp.). Source: Wehmeyer 1975; Connection: *Leptosphaeria spartinae* J.B. Ellis & B.M. Everhart (=*Coniothyrium* sp.). Source: Lucas and Webster 1967; Conidiogenesis: Annellidic. Conidia: Phaeoamerospores, phaeodidymospores.

Diplodina G.D. Westendorp (Coelomycete). Connection: *Leptosphaeria marcyensis* (C.H. Peck) P.A. Saccardo (=*Diplodina* sp.). Source: Lucas and Webster 1967. Conidiogenesis: Phialidic, periclinal thickening of apex of phialide, eustomatic. Conidia: Hyaline, 0- to 2-septate.

Hendersonia M.J. Berkeley. Nomina generica rejicienda. [=*Stagonospora* (P.A. Saccardo) P.A. Saccardo] (Coelomycete).

Leptophoma F. v. Höhnel (=*Phoma* P.A. Saccardo) (Coelomycete).

Microdiplodia A. Allescher (Coelomycete). Connection: *Leptosphaeria obtusispora* C.L. Spegazzini [=*Microdiplodia henriquesii* (F.

v. Thümen) F. Petrak & H. Sydow]. Source: Lucas 1963. Conidiogenesis: Unknown in *Microdiplodia henriquesii* (F. v. Thümen) F. Petrak & H. Sydow. Conidia: Phaeodidymospores.

Nakataea K. Hara (Hyphomycete). Connection: *Leptosphaeria salvinii* A. Cattaneo (=*Nakataea sigmoidea* K. Hara). Source: Ellis 1971. Conidiogenesis: Holoblastic, sympodial. Conidia: 3-septate, pale brown.

Pestalotia G. de Notaris (Coelomycete). Connection: *Leptosphaeria honiarensis* T. Matsushima (=*Pestalotia* sp.). Source: Matsushima 1971. Conidiogenesis: Annellidic. Conidia: Phaeophragmospores with appendages. Comments: *Leptosphaeria honiaraensis* may belong in *Pestalosphaeria* M.E. Barr (Amphisphaeriaceae) (Kendrick and DiCosmo 1979).

Pestalotiopsis R.L. Steyaert (Coelomycete). Connection: *Leptosphaeria elaeidis* C. Booth & J.S. Robertson. Source: Booth and Robertson 1961. Conidiogenesis: Holoblastic, annellidic. Conidia: Phaeophragmospores with appendages.

Phaeoseptoria C.L. Spegazzini (Coelomycete). Connection: *Leptosphaeria culmifraga* (E.M. Fries:E.M. Fries) V. Cesati & G. de Notaris (=*Phaeoseptoria* sp.). Source: Wehmeyer 1975; Connection: *Leptosphaeria fuckelii* G. Niessl v. Mayendorf (=*Phaeoseptoria* sp.). Source: Webster and Hudson 1957, Sivanesan 1984; Connection: *Leptosphaeria lactuosa* G. Niessl v. Mayendorf (=*Phaeoseptoria* sp.). Source: Webster and Hudson 1957, Sivanesan 1984; Connection: *Leptosphaeria macrospora* (L. Fuckel) F. v. Thümen (=*Phaeoseptoria* sp.). Source: Lucas and Webster 1967; Connection: *Leptosphaeria microscopica* P.A. Karsten [=*Phaeoseptoria airae* (W.B. Grove) R. Sprague]. Source: Sivanesan 1984; Connection: *Leptosphaeria nigrans* (M.R. Roberge) V. Cesati & G. de Notaris (=*Phaeoseptoria* sp.). Source: Hughes 1949, Sivanesan 1984; Conidiogenesis: Holoblastic. Conidia: Phaeophragmospores.

Phoma P.A. Saccardo (Coelomycete). Connection: *Leptosphaeria acuta* L. Fuckel (=*Phoma acuta* L. Fuckel). Source: Grove 1935; Müller and Tomaševič 1957; Connection: *Leptosphaeria agnita* (J. Desmazières) V. Cesati & G. de Notaris (=*Phoma* sp.). Source: Lucas and Webster 1967, Sivanesan 1984; Connection: *Leptosphaeria albopunctata* (G.D. Westendorp) P.A. Saccardo (=*Phoma* sp.). Source: Sivanesan 1984; Connection: *Leptosphaeria conferta* G. Niessl v. Mayendorf ex P.A. Saccardo (=*Phoma* sp.). Source: Lucas 1963, Sivanesan 1984; Connection: *Leptosphaeria congesta* M.T. Lucas (=*Phoma* sp.). Source: Lucas 1963; Connection: *Leptosphaeria cruenta* P.A. Saccardo (=*Phoma sanguinolenta* E. Rostrup). Source: Grove 1935; Connection: *Leptosphaeria doliolum* (C.H. Persoon:E.M. Fries) subsp. *doliolum* var. *doliolum* V. Cesati & G. de Notaris (=*Phoma hoehnelii* H.A. Van Kerstern subsp. *hoehnelii* var. *urticae* G.H. Boerema & H.A. Van Kerstern). Source: Lucas and Webster 1967, Boerema 1976; Connection: *Leptosphaeria dumetorum* G. Niessl v. Mayendorf (=*Phoma* sp.). Source: Lucas and Webster 1967; Connection: *Leptosphaeria haematites* M.R. Roberge ex J. Desmazières) G. Niessl v. Mayendorf (=*Phoma* sp.). Source: Lucas and Webster 1967, Sivanesan 1984; Connection: *Leptosphaeria libanotis* (L. Fuckel) G. Niessl v. Mayendorf (=*Phoma* sp.). Source: Lucas and Webster 1967, Sivanesan 1984; Connection: *Leptosphaeria lindquistii* M.J. Frezzi (=*Phoma macdonaldii* G.H. Boerema). Source: Sivanesan 1984; Connection: *Leptosphaeria maculans* (J. Desmazières) V. Cesati & G. de Notaris [=*Phoma lingam* (H.J. Tode:E.M. Fries)]. Source: Müller and Tomaševič 1957, Sivanesan 1984; Connection: *Leptosphaeria millefolii* (L. Fuckel) G. Niessl v. Mayendorf (=*Phoma* sp.). Source: Müller and Tomaševič 1957; Connection: *Leptosphaeria ogilviensis* (M.J. Berkeley & C.E. Broome) V. Cesati & G. de Notaris (=*Phoma* sp.). Source: Müller 1971; Connection: *Leptosphaeria pontiformis* (L. Fuckel) P.A. Saccardo (=*Phoma* sp.). Source: Webster and Hudson 1957, Wehmeyer 1975; Connection: *Leptosphaeria purpurea* H. Rehm (=*Phoma sanguinolenta* W.B. Grove). Source: Lucas and Webster 1967, Sivanesan 1984; Connection: *Leptosphaeria sacchari* H.J. Van Breda De Haan (=*Phoma* sp.; as *Phyllosticta* sp.). Source: Hudson 1960; Connection: *Leptosphaeria solani* L.G. Romell (=*Phoma* sp.). Source: Lucas and Webster 1967; Connection: *Leptosphaeria spartinae* J.B. Ellis & B.M. Everhart (=*Phoma* sp.). Source: Sivanesan 1984; Connection: *Leptosphaeria submaculans* L. Holm (=*Phoma* sp.). Source: Lucas and Webster 1967; Connection: *Leptosphaeria thomasiana* P.A. Karsten (=*Phoma* sp.). Source: Zeller 1927 (by association), Lucas and Webster 1967 (unnamed); Connection: *Leptosphaeria typhicola* P.A. Karsten (=*Phoma* sp.). Source: Lucas and Webster 1967 (unnamed), Sivanesan 1984; Conidiogenesis: Phialidic with periclinal thickening of apex of phialide. Conidia: Phaeoamerospores.

Scolecosporiella F. Petrak (Coelomycete). Connection: *Leptosphaeria macrospora* (L. Fuckel) F. v. Thümen [=*Scolecosporiella bernardiana* (P.A. Saccardo) A. Sivanesan]. Source: Sivanesan 1984; Connection: *Leptosphaeria typharum* (J. Desmazières) P.A. Karsten [=*Scolecosporiella typhae* (C.A. Oudemans) F. Petrak]. Source: Sivanesan 1984; Conidiogenesis: Holoblastic. Conidia: Pale brown, 3- to many-septate, cylindrical.

Septoria P.A. Saccardo (Coelomycete). Connection: *Leptosphaeria avenaria* G.F. Weber (=*Septoria avenae* B. Frank). Source: Grove 1935, Sivanesan 1984; Connection: *Leptosphaeria maydis* G.L. Stout (=*Septoria zeae* G.L. Stout). Source: Stout 1930 (by association); Connection: *Leptosphaeria nodorum* E. Müller [=*Septoria nodorum* (M.J. Berkeley) M.J. Berkeley]. Source: Lucas and Webster 1967, Sivanesan 1984; Connection: *Leptosphaeria phlogis* C.A. Oudemans (=*Septoria phlogis* P.A. Saccardo & C.L. Spegazzini). Source: Grove 1935 (by association); Connection: *Leptosphaeria sorbi* A.L. Jaczewski (=*Septoria sorbi* W.G. Lasch). Source: Grove 1935 (by association); Conidiogenesis: Three types of conidiogenesis have been found for the pathogenic species of *Septoria* studied thus far. They are (1) holoblastic, sympodial, (2) simple holoblastic, and (3) phialidic with periclinal thickening of the apex of the phialide. Conidiogenesis has not been determined for any of the *Septoria* anamorphs of *Leptosphaeria*. Conidia: Hyaline, multiseptate, filiform.

Stagonospora (P.A. Saccardo) P.A. Saccardo (Coelomycete). Connection: *Leptosphaeria anemones* L. Hollós (=*Stagonospora anemones* N.T. Patouillard). Source: Sivanesan 1984; Connection: *Leptosphaeria arundinaceae* P.A. Saccardo (=*Stagonospora vexata* P.A. Saccardo). Source: Grove 1935 (by association); Connection: *Leptosphaeria bicolor* D.L. Hawksworth, W. Kaiser & B.N. Ndimande (=*Stagonospora* sp.). Source: Kaiser et al. 1979; Connection: *Leptosphaeria cistina* M.J. de Urríes y Azara (=*Stagonospora* sp.; as *Hendersonia cisti* M. de Sousa da Camara). Source: Lucas 1968; Connection: *Leptosphaeria dumetorum* G. Niessl v. Mayendorf (=*Stagonospora* sp.; as *Hendersonia* sp.). Source: Lucas and Webster 1967, Sivanesan 1984; Connection: *Leptosphaeria eustomoides* P.A. Saccardo (=*Stagonospora* sp.; as *Hendersonia* sp.). Source: Webster and Hudson 1957; Connection: *Leptosphaeria gigaspora* G. Niessl v. Mayendorf (=*Stagonospora gigaspora* P.A. Saccardo). Source: Grove 1935 (by association); Connection: *Leptosphaeria libanotis* (L. Fuckel) G. Niessl v. Mayendorf (=*Stagonospora* sp.; as *Hendersonia* sp.). Source: Wehmeyer 1975; Connection: *Leptosphaeria polygonati* E. Müller & M. Tomaševič (=*Stagonospora* sp.; as *Hendersonia* sp.). Source: Müller and Tomaševič 1957; Connection: *Leptosphaeria pontiformis* (L. Fuckel) P.A. Saccardo (=*Stagonospora* sp.; as *Hendersonia* sp.). Source: Lucas and Webster 1967, Sivanesan 1984; Connection: *Leptosphaeria pratensis* P.A. Saccardo & P.A. Briard [=*Stagonospora melioti* (W.G. Lasch) F. Petrak]. Source: Jones and Weimar 1938, Lucas and Webster 1967; Connection: *Leptosphaeria taiwanensis* W.Y. Yen & C.C. Chi (=*Stagonospora taiwanensis* W.H. Hsieh. Source: Hsieh 1979, Sivanesan 1984; Connection: *Leptosphaeria viridella* (C.H. Peck) P.A. Saccardo (=*Stagonospora* sp.; as *Hendersonia*). Source: Lucas and Webster 1967; Conidiogenesis: Holoblastic, sometimes annellidic. Conidia: Hyaline, multiseptate, cylindrical.

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Our Living Heritage: The Biological Resources of Illinois

Edited by
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Michael R. Jeffords
Illinois Natural History Survey

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Foreword

We live in a world of near continuous monitoring. In our automobiles we monitor the status of fuel, oil pressure, temperature, and seat belts through gauges, lights, and electronic voices. The consumption of electricity and fuel in our homes is monitored as is the chlorine in our drinking water and the alcohol in our beer. Manufacturers retain quality assurance inspectors and issue warrantees and guarantees to convince us that all is well. We monitor our schools and measure our own progress through grades and proficiency scores. It seemed appropriate, therefore, that the Illinois Natural History Survey should take a measure of the living natural resources of Illinois by bringing together a knowledgeable group of persons to summarize the state of the State. In order to share this information and to provide an opportunity for discussion, a symposium, "Our Living Heritage: The Biological Resources of Illinois," was sponsored by the Illinois Department of Energy and Natural Resources and organized by the Survey. The event, timed to coincide with Earth Day 1990 celebrations, was held on April 23 and 24 on the campus of the University of Illinois at Urbana-Champaign. It was attended by nearly 250 professional scientists from some 50 agencies and institutions along with a number of interested and dedicated citizens. To share the results of that symposium with an even larger audience, we have issued this publication of its proceedings.

To address the salient features of the living resources of Illinois in an ordered fashion, the symposium was presented in five sessions: forests, prairies and barrens, wetlands, streams and caves, and agro-urban ecology. When we consider that only 0.5% of Illinois remains in undisturbed natural areas, that Illinois ranks 46th among states in publicly owned open space per person, that forest acreage has decreased by 73% in the past century and tallgrass prairie by over 99%, that 85% of our wetlands have been lost, that soil erosion proceeds at the rate of 200 million tons per year, and that approximately 30,000 tons of herbicide and 3,500 tons of insecticides are used annually on agricultural crops in Illinois, we can scarcely imagine the tone of the symposium to have been anything but pessimistic. In part, there was discouragement, but it was tempered by positive developments, including the designation of the Middle Fork of the Vermilion River as a National Wild and Scenic River, the acquisition of the Cache River Basin, the initiation of a study to identify high-quality Illinois streams based on biodiversity, and the ever quickening actions of the Nature Preserves Commission.

Preservation/conservation has been in conflict with consumption/development since the days of Theodore Roosevelt. At times one side seems to prevail over the other, but the balance has been clearly on the side of consumption. Special interest groups have to a considerable extent managed to give the word *environmentalist* a pejorative cast and the word *development* a positive ring. During the past decade, the executive branch of the federal government has determinedly downplayed environmental concerns, and that stance has been translated into inertia in a number of federal agencies with responsibility for natural resources. The focus of the United States Environmental Protection Agency, for example, has until very recently ignored the living components of the environment. At the same time, public sensitivity to environmental concerns has dramatically increased, primarily through public service television and other media-generated presentations on tropical deforestation, extinction of species, depletion of the ozone layer, agro-chemical contamination of groundwater, and the effects of acid rain. Some of this concern is now being transformed into political action. Polls suggest

that the public understanding of environmental matters is quite high, and some believe that it exceeds the perceptions of elected officials. A Green Party has emerged in this country only very recently, but Greens are a part of both major political parties and the trend in federal legislation may soon begin to sway in favor of conservation/preservation and away from consumption/development. The National Institutes for the Environment may well become a reality within the next several years. Within this tentatively encouraging national picture, the symposium was timely indeed.

One symposium event of special interest cannot be documented in these proceedings—the "citizens respond" program of Monday evening, April 23—and I would like to note it here. Michael Jeffords and Susan Post of the Survey opened that session with a mulitmedia presentation on the biodiversity of Illinois. Their slides of representative plants and animals and habitats of the natural divisions of Illinois brought home to us the beauty and fragility that can yet be discovered in the landscape of our state. A panel presentation by five environmental activists followed: Clark Bullard, Office of Energy Research at the University of Illinois at Urbana-Champaign; Max Hutchison, Natural Land Institute of The Nature Conservancy; Lawrence Page of the Illinois Natural History Survey; Donna Prevedell, farmwife and contributing editor to the *Progressive Farmer*; and Michael Reuter, Volunteer Stewardship Network of The Nature Conservancy. They spoke briefly but openly on preservation activities in which they had been closely involved. The discussion was then turned over to the audience, who asked questions and shared their experiences—successes and failures—with preservation efforts.

I urge you to read on in order to understand the status of the biological resources of Illinois and to appreciate how much remains to be accomplished to secure their future—and ours. I would be remiss, however, if I did not conclude by acknowledging the committee of Survey staff who planned and conducted the symposium: Lawrence Page, Michael Jeffords, Joyce Hofmann, Susan Post, Louis Iverson, and Audrey Hodgins. Their efforts included developing the program, arranging for speakers and facilities, producing and mailing promotional materials, and welcoming the audience. Without their enthusiasm and hard work, the symposium would not have materialized and our understanding of the biological resources of Illinois would be much diminished.

Lorin I. Nevling, Chief
Illinois Natural History Survey

Contents

Introduction

The term *biodiversity* has not yet made its way into most dictionaries, but the word is generally accepted to mean the organisms that inhabit the Earth and the ecosystems in which they live. Lying at the junction of the eastern forest, western great plain, southern coastal plain, Ozark uplift, and northern forest biomes, Illinois provides habitat for an extremely varied native flora and fauna. Scientists at the Illinois Natural History Survey recently compiled data on the biodiversity of Illinois and conservatively estimated that more than 53,000 species are native to the state (Appendix I). The largest groups are insects with about 17,000 species and fungi with about 20,000 species. In addition, Illinois is home to 2,068 species of vascular plants and 649 species of vertebrates (mammals, birds, reptiles, amphibians, and fishes).

The biodiversity of Illinois is more readily appreciated when it is compared to that of other regions. Consider, for example, that the Pine Hills–LaRue Swamp region of southwestern Illinois contains about 1,000 native species of plants. The Great Smoky Mountains National Park, an area of wilderness about 260 times larger, contains only 1,200 native plant species. That same region of southwestern Illinois also has more amphibian and reptile species (61) than are found in any region of comparable size in the United States. Perhaps equally surprising, one-fourth of all the freshwater fishes and mussels of North America north of Mexico are found in Illinois.

The destruction of tropical rainforests, which are thought to contain over half the total species of organisms, has been widely publicized, but all ecosystems are threatened as human populations and their support systems expand. Illinois, one of the most altered regions on Earth, is experiencing an ongoing and accelerating loss in variety as well as absolute numbers of organisms. At least 115 species are known to have been extirpated in recent decades (Appendix I), and another 497 are officially listed in Illinois as threatened or endangered. Unless circumstances change dramatically, Illinois will soon have lost 1 in 5 of its native species of fishes, 1 in 5 of its native flowering plants, 1 in 5 of its native birds, 1 in 4 of its native mammals, and a startling one-half of its native freshwater mussels!

Historical accounts of Illinois noted huge trees, vast grasslands, and extensive wetlands. Illinois was chiefly a combination of flat, mesic, "marshy" prairies and forested hilly country. Interspersed in these habitats were sand dunes, bogs, fens, sedge meadows, savannas, and swamps. Unfortunately, little of that original landscape remains. In fact, Illinois ranks an unenviable 49th among states in the percentage of natural areas surviving. Of the original 22 million acres of prairie, only 2,300 acres (0.01%) remain. Of the 14 million acres of forest present in Illinois in 1820, only 13,500 acres of primary (undisturbed) forest survive (0.10%). Many of our wetlands have been, and continue to be, drained before they can be biologically inventoried and their value determined. Our streams are polluted and increasingly degraded by the influx of soil from surrounding farmland. A significant portion of the biodiversity of Illinois will soon disappear unless the remaining species-rich areas are protected.

Several factors contribute to the global loss of biodiversity: the explosive growth of the human population, widespread and extreme poverty and malnutrition, and a notable lack of sustainable, productive agricultural and forest systems in many regions of the world. This loss is of paramount importance because human existence depends on the biological resources of the planet. Our prosperity and well-being are based largely on our ability to take advantage of the properties of plants, animals, and microorganisms for

food, clothing, medicine, and shelter. As species are lost, we reduce our options for future development of vital commodities. As habitats and ecosystems are lost, we lose the recreational potential of wild places, and we disturb the balance of atmospheric gases, including oxygen, carbon dioxide, and ozone. Although the link between biodiversity and human survival is clear, we must also learn to value the biodiversity of our planet and state for its own sake, quite apart from direct benefits to us.

The loss of biodiversity is a global problem, but the loss of Illinois biodiversity is of special concern to Illinoisans. In our state, the major cause of the loss of species is the destruction and degradation of habitat. The anthropogenic changes associated with agriculture and urbanization cause environmental degradation and lead to the extinction of species. If the loss of its native biodiversity is not halted, Illinois could become a biological desert unable to respond to the need for new products and incapable of developing resource-based solutions to human problems. At issue is how we will protect the natural habitats that remain, restore some of the natural areas that have been lost, and balance the protection of biodiversity against conflicting social and economic interests. If we are to make informed decisions, we must first complete the following tasks.

Inventory the biological resources of Illinois. Our knowledge about the biodiversity of Illinois is incomplete. This lack of information hampers our ability to estimate the size and nature of the problem and to recommend remedial measures. We are unable to identify all the biological resources at risk because no inventory of all life forms exists. Although our knowledge of some taxa is extensive, other groups are largely unknown. Species are lost before they are discovered and studied. Even in groups that are well studied (e.g., birds and fishes), changes are occurring so rapidly that additional data are needed if wise decisions relative to development and management are to be made.

Develop the scientific base on which the emerging fields of conservation biology, restoration ecology, and environmental management can be built. Recent global and regional environmental changes and the inevitability of future modifications underscore the need for prudent decisions regarding the protection and use of natural resources. Indices are needed that will enable us to compare habitats and select outstanding natural areas for management and protection.

Educate Illinoisans regarding the importance of biological diversity. Biodiversity is of particular interest to biologists and ecologists, but all citizens must be informed about the global biodiversity crisis if protective legislation is to be enacted and funding ensured.

Encourage socio-economic research related to the wise use of biodiversity. We need theoretical and empirical studies on the economic and social causes of the biodiversity crisis, its consequences, and its remedies.

Sponsored by the Department of Energy and Natural Resources and the Illinois Natural History Survey, the symposium "Our Living Heritage: The Biological Resources of Illinois" was held in celebration of Earth Day 1990 on the Urbana-Champaign Campus of the University of Illinois. Two days, April 23 and 24, were spent reviewing present information about the biodiversity of Illinois and identifying actions necessary to understand and conserve the remaining resources of our state. Sessions were arranged by ecosystem (forests, prairies and barrens, wetlands, streams, caves, and agro-urban habitat), and contributors discussed what is known about how these ecosystems function, how they have been modified, and how various decisions are likely to affect their survival. The proceedings that follow summarize information on the biodiversity of Illinois and suggest where additional research is needed. Nineteen of the twenty-two presentations delivered at the symposium are included here, either as abstracts or papers.

Although the audience agreed that more information on certain subjects and groups of organisms is needed, they also acknowledged that we know enough to conclude that we have already drastically altered most of our native landscape and that we are rapidly losing native species. Without greater protection and more extensive management of natural areas, the loss of habitats and species can only accelerate.

Session One: Forests

Like the first farmsteads, towns of the frontier were built in stumpland meadows. The trees were gone. The civic landscapes sweltered in the sun. Never so quick an afterthought: fast-growing black locust trees were imported and planted everywhere, from college campuses to courthouse squares, to provide a promise of shade. What irony—the sons of the world's most incredible axemen planting seedlings in the shadow of stumps five feet across.—Robert O. Petty

In 1820, approximately 13.8 million acres of Illinois were forested. The midcontinental location of the state and its north to south distance of nearly 400 miles allowed an unusual variety of forest types to exist. The pre-settlement forests of Jo Daviess County covered nearly 80% of the land surface and were noted for their rugged topography and the presence of Pleistocene relic species. In 1830, a U.S. Government geologist surveying the Grand Prairie Division in central Illinois observed, "Sometimes the woodland extends along this river for miles continuously, again it stretches in a wide belt off into the country, marking the course of some tributary streams, and sometimes in vast groves of several miles in extent, standing alone, like islands in the wilderness of grass and flowers." Robert Ridgway, a Smithsonian naturalist, noted the immense size and diversity of the trees along the lower Wabash Valley in the 1870s. With photographs and measurements, he documented the extraordinary nature of the bottomlands. In the Shawnee Hills the relatively broad, flat-bottomed ravines, originally cut by the melt-waters of the Illinoian glacier, were verdant, damp jungles filled with trees—beech, sugar maple, and tulip—that reached and overtopped the sandstone bluffs. South of the Shawnee Hills the terrain flattened and a distinctly southern forest grew in the past and present Ohio River valleys. Great expanses of bald cypress–water tupelo swamps filled the lowlands along the Cache and Ohio rivers. Rare species like willow oak, silverbell, water hickory, and American chestnut occupied river terraces, flatwoods, and ravines.

We know of these magnificent forests for several reasons. Early settlers to Illinois, while greatly impressed with the vast expanse of prairie, chose to live in the woodlands, a landscape with which Europeans felt more familiar. Thus the nature of these forests came to be better documented than that of other landscape types. In addition, early biologists like Ridgway and the St. Louis physician George Engelmann described the presettlement condition of Illinois forests in considerable detail.

To begin to understand the current condition of Illinois forests we must reflect upon their past and on what has been lost. Robert Ridgway, writing in the *American Naturalist* in the 1870s, described the forests along the Wabash River. "If the forest is viewed from a high bluff, it presents the appearance of a compact, level sea of green, apparently endless . . . the tree-tops swaying with the passing breeze, and the general level broken by occasional giant trees which rear their massive heads so as to overlook the surrounding miles of forest . . . while the occasional, and by no means infrequent, 'monarchs' which often tower apparently for one-third their height above the tree-top line, attain an altitude of more than one hundred and eighty feet, or approach two hundred feet." In the visitor center of Beall Woods, an Illinois Nature Preserve in Wabash County, an immense yellow outline painted on the floor represents one of these last great trees. The circle is seventeen feet in diameter.

Today nearly 4.3 million acres of trees can be found in Illinois, not too startling a decline in acreage from 1820 if we consider the agricultural and urban development that now blankets the state. Lest we are too complacent, however, we should recall that much of the forest acreage of today is second- or third-growth timber or pine plantations; only 13,500 acres of relatively undisturbed forests remain—a shockingly small percentage of our rich, forested heritage. Fortunately, fragments remain of nearly all forest types found in

presettlement times and these, in conjunction with land survey records, early written accounts, and good biological detective work, allow us to mentally reconstruct, and sometimes physically restore, the various forest habitats. These efforts, to some extent, provide a glimpse of what was once Illinois.

The three papers given at this session help us to conceptualize the forests that were once so integral to the Illinois landscape and to understand how the forests that exist today came to be. In addition, they enable us to appreciate the role that forests play in the economy of the state, in preserving biodiversity and habitat for wildlife, in controlling erosion and improving the quality of surface water, and in conserving energy and slowing global warming.

Forest Resources of Illinois: What Do We Have and What Are They Doing for Us?

Louis R. Iverson, Illinois Natural History Survey

Forests occupy only a relatively small proportion (12%) of the land area of Illinois (Figure 1), yet they provide tremendous benefits to the citizens of the state. We need only walk through the woods to be aware of some of these benefits: aesthetic beauty, habitat for specialized plants and for birds and other wildlife, recreational opportunities, and high-quality hardwood. The more subtle but equally important benefits that forest ecosystems provide, however, are not so readily perceived. Forested acres, for example, dramatically inhibit soil erosion, thereby reducing the sediment load that eventually finds its way into our water courses; no forest benefit is more important when we consider that 3.3 pounds of soil are lost for each pound of grain produced in Illinois (Iverson et al. 1989). Global warming, due largely to the excessive buildup of carbon dioxide in the atmosphere, is also counteracted to some degree by our forests because plants convert tremendous quantities of carbon dioxide into plant tissue and oxygen each day. Then too, our forests contribute greatly to the maintenance of biological diversity, a benefit of crucial importance in Illinois where the landscape is dominated by a row-crop monoculture.

The purpose of this paper is to review the historic trends that shaped the Illinois forest, to document its present status, and to summarize the benefits it currently provides. The material is largely condensed from a more detailed and complete document, *Forest Resources of Illinois: An Atlas and Analysis of Spatial and Temporal Trends* (Iverson et al. 1989). Readers are encouraged to consult that book and the map (Iverson and Joselyn 1990) that accompanies it for a great deal more information regarding the forests of Illinois, including data specific to the counties in which they may be particularly interested. Both the book and map are available as Special Publication 11 from the Illinois Natural History Survey.

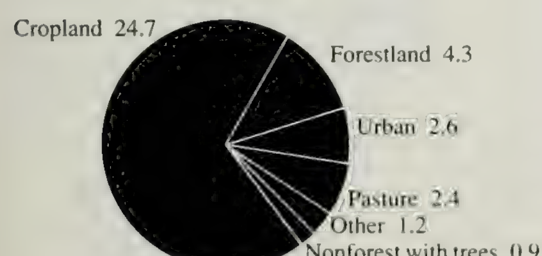

Figure 1. Major land use in Illinois in millions of acres, 1985. Total acres in Illinois = 36,061,000. Source: Hahn 1987.

Much of the story of the Illinois forests can be understood by comparing the earliest systematic vegetation data available for the state, data recovered from the original land surveys made during the first half of the nineteenth century, with recent land-use information taken via remote sensing from airplanes and satellites.

FORESTS OF 1820

Illinois was surveyed by the United States General Land Office between 1807 and 1844. Starting from southern Illinois and working northward, surveyors divided the land into townships and sections, prepared plat maps, and made notes on the vegetation they encountered. These records provide a fairly complete picture of the landscape prior to the massive disturbance caused by European settlement. Anderson (1970) published a map showing the statewide distribution of forest and prairie as deduced from these data (Figure 2). Large expanses of forest existed, primarily in the south and west. Approximately 38.2% of the state (13.8 million acres) was forested at the time of the European settlement, 61.2% was prairie, and 0.6% was water. Fifteen counties were at least 80% forested, and only 21 counties had less than 20% forest cover.

FOREST TRENDS 1820–1980

Illinois forests have undergone drastic changes in the decades since European settlement. Only 31% of the forest area present in 1820 exists today (Figure 3). The lowest percentage of forest occurred about 1920 when only 22% of the land forested in 1820 remained in forest (Telford 1926; U.S. Forest Service 1949; Essex and Gansner 1965; Hahn 1987). Although forest area has increased in recent decades, most of today's forest is secondary forest, and only about 11,600 acres exist in a relatively undisturbed condition (Illinois Natural Areas Inventory as reported in Iverson et al. 1989). Illinois ranks 49th, next to Iowa, in percent of the state converted from its "potential" vegetation type (Küchler 1964); only 11 percent of the state remains in its "potential" vegetation type and essentially all of that is forest (Klopatek et al. 1979).

The pattern of deforestation of the primary (i.e., "virgin") forests of Illinois can be deduced to some degree by relying on estimates of forestland in 1820 and 1924 and on other written accounts (especially Telford 1926). From initial settlement in the early 1800s to 1860, agriculture was the only important industry associated with wooded lands. Until 1830, forests were the sole source of potential agricultural land; however, when settlers realized that the prairies made good cropland and after the invention of the moldboard plow, the prairies were converted to cropland at an astonishing rate of approximately 3.3% per year (Table 1). Over 300,000 people settled the prairies during the decade of the 1830s, and this burgeoning population created an enormous demand for housing material, fuel, and fence posts. Railways were not yet in place to import lumber, and most of the timber in the prairie counties rapidly disappeared.

Figure 2. Forests in Illinois about 1820. Source: Anderson 1970.

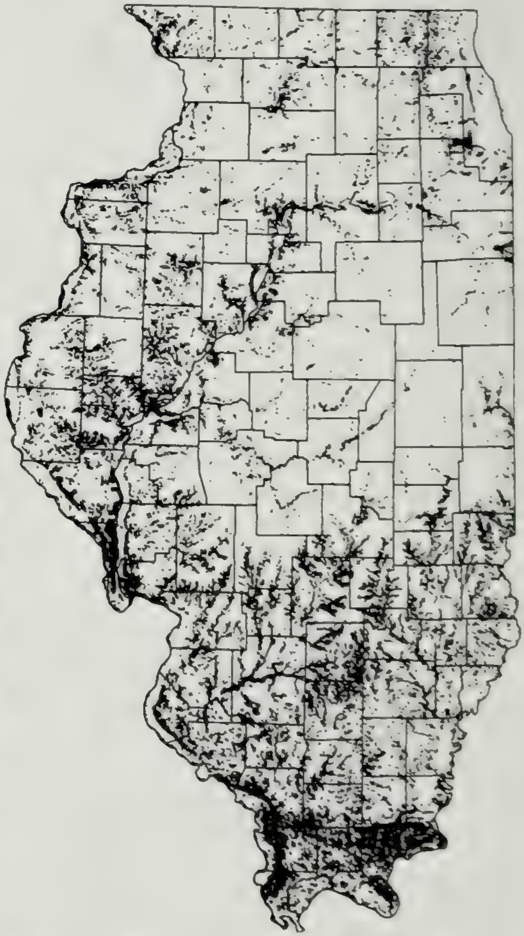

Figure 3. Forests in Illinois about 1980. Source: U.S. Geological Survey land-use data, 1973–1981.

By 1860, a timber industry had begun to flourish in Illinois. Ninety-two of the 102 counties had industries based on wood products by 1870, and forestland had dwindled to 6.02 million acres (Telford 1926). During the 1880s, annual lumber production exceeded 350 million board feet, 2.2 times the present production, and continued to increase until 1900, when it began to decrease as the resource itself declined. By 1923, only 22,000 acres of the original 13.8 million acres of primary forest remained.

A useful comparison can be made between deforestation in Illinois in the nineteenth century and the deforestation presently under way in the tropics. The primary forests of Illinois went from 13.8 million acres in about 1820 to 6 million acres in about 1870, to 22,000 acres in about 1920 (Figure 4), an overall deforestation rate of 1% per year (1.13% of the original primary forest lost during the first half of the century, 0.87% during the second half). Deforestation rates, however, were not a constant during the period and probably followed a curve such as that shown in Figure 5, with maximum deforestation in the late 1800s. Rates of deforestation have also been compiled for Rondônia in Brazil (Malingreau and Tucker 1988), for Costa Rica (Sader and Joyce 1988), and for Malaysia (Iverson et al. 1990) and are shown in Table 1. The fastest rate, 2.47% annually, was found from 1972 to 1982 in peninsular Malaysia, even though more forestland was being removed in Rondônia. This rate was probably equaled in Illinois in the late 1800s (Figure 5). A similar curve is currently found in the other countries, with Malaysia at the apex of the curve, Rôndonia on the upward slope with increasing rates, and Costa Rica on the downward slope with a declining resource and a dropping rate. History does indeed repeat itself, and we Americans should acknowledge our own history of deforestation as we now attempt to curb the destruction of tropical forests.

FOREST TRENDS 1962–1985

Forest area increased by 10% from 1962 through 1985, from 3.87 to 4.26 million acres. This increase is partially explained by the reduced number of cattle raised in Illinois and the conversion of pastures and hayland to secondary forest. Total net volume of growing stock has also increased 40% since 1962 (Table 2). Pine plantations have shown the highest percentage of increase in volume (up to 375%), but the largest absolute increase in volume was shown by oaks (an increase of 0.64 million cubic feet).

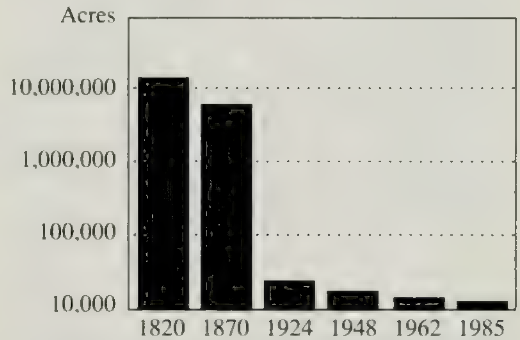

Figure 4. Extent of Illinois primary forests, 1820–1985. Interpreted from Telford 1926; U.S. Forest Service 1949; and Anderson 1970.

Table 1. Recent rates of land clearing in three tropical countries compared with rates of land clearing in Illinois from 1820 to 1923.

Location	Land use	Year	Sq km of land	Percent cleared per year
Rondônia, Brazil	Forest	1978	239,800	
		1987	208,000	1.47
Malaysia	Forest	1972	48,970	
		1982	36,870	2.47
Costa Rica	Forest	1940	34,210	
		1983	8,710	1.73
Illinois	Forest	1820	55,870	
		1870	24,290	1.13
		1923	90	0.87
Illinois	Prairie	1830	87,550	
		1860	10	3.33

Compositional changes during 1962–1985 were especially profound, with vast percentage increases in commercial acreage of white, red, and jack pines, oak–gum–cypress, and especially maple–beech forest types (Figure 6). Maples increased 41-fold in the past 25 years—from 0.025 million acres to 1.046 million acres! Concomitantly, oak–hickory decreased by 337,000 acres (14%), and over half of the state's elm–ash–soft maple disappeared. The loss of oak–hickory is largely from maple "take-over" as shade-tolerant maples replace oak–hickory stands following mortality or harvest. A documented case of the maple take-over of a forest in east-central Illinois is presented later in these proceedings (Ebinger and McClain, page 375) and elsewhere (Ebinger 1986). The reduction of elm–ash–soft maple is due to mortality from Dutch elm disease and the conversion to cropland of bottomland forests that once supported this forest type. These data make clear that although forest acreage and volume have increased since 1962, the quality and value of the timber resource has diminished, at least by today's standards. Maple-dominated forests also support a somewhat different array of wildlife than that supported by oak-dominated forests, and such "hard mast" (acorns and hickory nuts) feeders as squirrels and woodpeckers are less abundant in maple-dominated forests.

ILLINOIS FORESTS TODAY

A closer look at the current status of the Illinois forests reveals some interesting and on occasion surprising information.

Area

Estimates of current forestland compiled from the 1985 U.S. Forest Service inventory indicate that about 12% (4.27 million acres) of the land area of Illinois is forested (Hahn 1987). The extent of this forestland can be seen in Figure 3 (as well as in several forms on the 1:500,000 scale map of Iverson and Joselyn 1990). The importance of the southern and western counties is clear. At one extreme is Ford County with only 3,000 acres of forestland; at the other is Pope County with 149,200 acres, Jackson with 134,500, and Pike with 122,500. Included in this 4.27 million acres are 4,029,900 acres of commercial (capable of and potentially available to produce commercially valuable trees) forestland and 235,600 acres of reserved or protected timberland.

Wooded strips less than 120 feet wide and land on which at least one tree (5 inches in diameter at breast height) occurs per acre make up a category that has been designated "nonforestland with trees." Included in this category are wooded strips (178,500 acres), wooded pastures (162,400), urban and other built-up land (139,500), windbreaks (133,100), improved pastureland with trees (103,600), urban forest (102,800), and several miscellaneous classes. Taken together, 900,800 acres of nonforestland with trees are found in Illinois.

Composition

The composition of many Illinois forests has changed over the past several decades. Today, about one-half of the commercial forest acreage

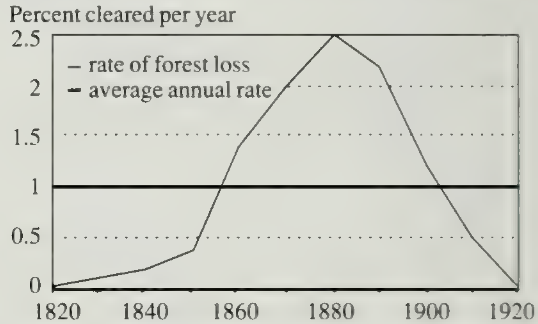

Figure 5. Rate of forest clearing in Illinois, 1840–1920. Interpreted from Telford 1926; U.S. Forest Service 1949; and Anderson 1970.

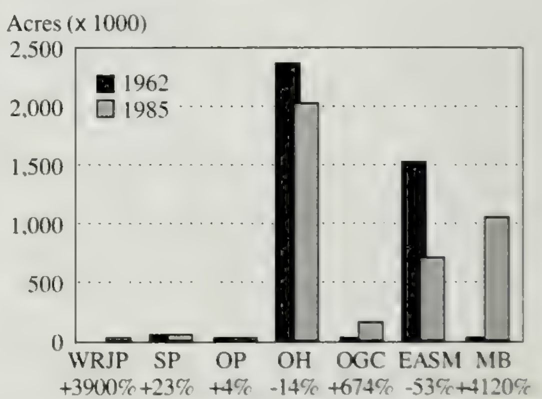

Figure 6. Composition of Illinois commercial forests, 1962–1985. Percent change is given below each pair of bars. Abbreviations are decoded as follows: WRJP = white–red–jack pine, SP = shortleaf pine, OP = oak–pine, OH = oak–hickory, OGC = oak–gum–cypress, EASM = elm–ash–soft maple, MB = maple–beech. Source: Hahn 1987.

Table 2. Net volume of growing stock on commercial forestland in Illinois by species group for 1962 and 1985, percent change between those dates, and net annual growth estimated from 1985 data.

Species group	1962 (thousand cubic feet)	1985 (thousand cubic feet)	Percent change	Net annual growth (thousand cubic feet)
Softwoods				
Loblolly–shortleaf pine	15,200	64,700	+327	1,891
White pine[1]	—	16,800	—	393
Red pine[1]	—	12,000	—	310
Eastern red cedar	2,400	11,400	+375	445
Bald cypress	6,800	8,900	+31	13
Jack pine[1]	—	700	—	36
Other softwoods	700	3,000	+329	110
Total	25,100	117,500	+368	3,224
Hardwoods				
Red oak	701,800	1,062,400	+51	18,352
White oak	739,700	1,017,600	+38	15,075
Hickory	343,900	522,500	+52	7,443
Soft maple	259,200	341,600	+32	14,144
Elm	367,700	267,400	-27	-5,106
Green–white–black ash	218,200	261,000	+20	6,932
Hard maple	99,800	163,100	+63	3,717
Cottonwood	114,100	157,800	+38	1,976
Sycamore	123,300	134,600	+9	2,412
Black walnut	77,500	119,100	+54	2,279
Hackberry[2]	—	93,500	—	5,683
Black cherry[2]	—	87,700	—	3,663
Basswood	25,800	54,100	+110	1,215
Yellow poplar	26,400	51,800	+96	1,609
Willow[2]	—	50,300	—	1,427
Sweetgum	58,600	45,100	-23	1,163
River birch[2]	—	36,800	—	1,257
Tupelo	13,900	28,000	+101	209
Beech	14,500	12,100	-17	242
Butternut[2]	—	5,700	—	105
Aspen	9,100	1,900	-79	28
Other hardwoods	223,100	203,500	-9	8,966
Total	3,416,600	4,717,600	+38	92,791
Total all species	3,441,700	4,835,100	+40	96,015

[1] Tabulated only in 1985 survey, included with other softwoods in 1962.
[2] Tabulated only in 1985 survey, included with other hardwoods in 1962.
Source: Hahn 1987; reprinted from Iverson et al. 1989.

(2.03 million acres) is oak–hickory, one-fourth is maple–beech (1.05 million acres, almost exclusively sugar maple), and one-sixth is elm–ash–soft maple (0.72 million acres) (Figure 6). Together, the remaining forest types (white–red–jack pine, loblolly–shortleaf pine, oak–pine, and oak–gum–cypress) account for an additional 216,800 acres of commercial forestland.

The location of these various forest types has been mapped (Iverson et al. 1989; Iverson and Joselyn 1990). Oak–hickory is found throughout the state with maximum levels in the western and southern counties. Maple–beech, a forest type also found throughout Illinois, has the highest average number of acres per county in western Illinois but is proportionally most prominent in the central Grand Prairie counties. Elm–ash–soft maple is found in bottomland forests, and these forests are more frequently located in the southern counties. Oak–pine, oak–gum–cypress, and shortleaf pine types are confined to the southern counties, but the white pine type is most common in the western part of the state.

According to the Illinois Plant Information Network (Iverson and Ketzner 1988), 508 woody taxa have been recorded in Illinois, a

high diversity of woody plant species considering the extensive agricultural acreage. Trees account for 261 taxa, shrubs 284, and lianas 47 (some taxa include more than one type). These woody plants account for a diversity of cover types and occupy a variety of habitats. On average, 70 tree taxa and 54 shrub taxa have been recorded from each county (Iverson et al. 1989). Southern counties have the largest number of tree taxa (Jackson has 145 taxa, Pope 129, and Union 128), and northeastern counties have the most shrub taxa (Cook has 153 and Lake 136).

Volume, Annual Growth, and Number

Net volume estimates for 1985 showed the prominence of oak and hickory in commercial forests, with considerable amounts of ash, black walnut, cottonwood, elm, maple, and sycamore as well (Figure 7). The data shown in Figure 7 may have greater immediacy if we consider that 1 million board feet provide enough lumber to build an estimated 73 wood houses. The total net volume of Illinois timber in 1985—17.5 billion board feet—would theoretically build 1.3 million wood houses!

Total net volume estimates of growing stock were 4.8 billion cubic feet, an average of 47.4 million cubic feet per county or 1,200 cubic feet per acre of commercial forestland in the state. Hard hardwoods (predominately oak, hickory, and ash) accounted for 68% of total volume; soft hardwoods (e.g., elm and soft maple) accounted for 30% and softwoods (e.g., pine) made up 2%.

According to annual growth estimates for 1985 (Hahn 1987), growing stock showed 96 million cubic feet of growth, or 437 million board feet of sawtimber growth. Over 42% of net annual sawtimber growth was accounted for by oaks, with another 10% from soft maple, 6.3% from ashes, 3.7% from black cherry, 3.3% from hard maple, and 3.2% from black walnut. Only elm and black ash showed negative growth rates between 1962 and 1985, and these are attributed to Dutch elm disease and the clearing of bottomlands.

The estimated number of trees in Illinois commercial forests revealed a somewhat surprising statistic: the elms, with 344 million trees, were the most common group. Most of these, however, are small slippery (or red) elms with little commercial value (Figure 8). Overall, white oaks (99 million), red oaks (136 million), hickories (185 million), hard maples (117 million), and soft maples (91 million) were very abundant.

Age

Illinois forests are reasonably well distributed among age classes, with 61-year to 80-year classes most prevalent; however, certain trends appear when the ages of major forest types are considered (Figure 9). Oak–hickory forests show a very uneven age distribution, with the majority older than 60 years. A predominance of maple–beech is found in younger age classes (<30 years) relative to oak–hickory and elm–ash–soft maple. This pattern again illustrates, as it did in the data on acreage trends (Figure 6), two important aspects of Illinois forests today: maples are rapidly increasing in younger age classes and forest types dominated by oaks and elms are declining and have relatively fewer trees in younger age classes. Among the other forest types, white

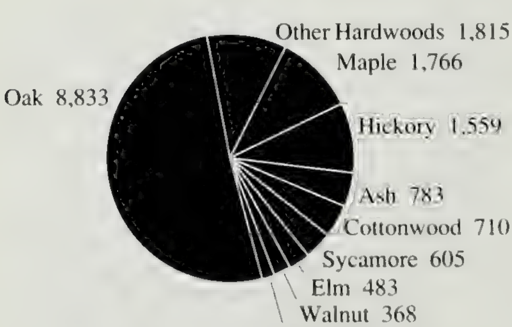

Figure 7. Total volume of Illinois commercial forestland in 1985 in million board feet. Total net volume of sawtimber was 17.5 billion board feet. Source: Hahn 1987.

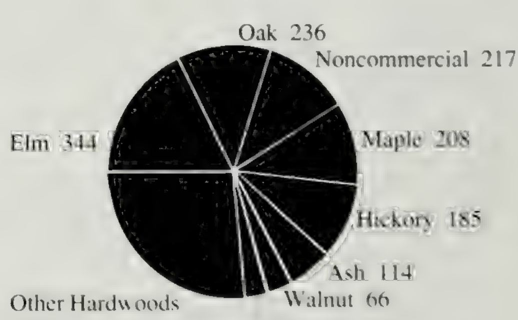

Figure 8. Number of live trees in 1985 in Illinois commercial forestland in millions of trees. Total number of trees was 1.93 billion. Source: Hahn 1987.

and shortleaf–loblolly pine peak in the 21- to 30-year class with very little stand acreage under 10 years of age. Pine plantations are no longer being planted to the extent they were from 1930 to 1960, primarily because of changes in the management of the Shawnee National Forest (U.S. Forest Service 1986).

Site

Forest stands can also be classified according to an index that measures the quality of a site based on the height its trees attain after 50 years of growth. The soils of Illinois are superior for forest growth compared to the relatively shallow or infertile soils of neighboring states like Missouri or Kentucky. According to this index, fully 84% of the trees in the commercial forestlands of Illinois are capable of supporting growth of 61 to more than 100 feet during a 50-year interval.

Mortality

In 1985, the forests of Illinois experienced an annual mortality of over 200 million board feet of sawtimber (67 million cubic feet of growing stock) (Hahn 1987). In contrast, 161 million board feet of timber were cut in 1983 (Blyth et al. 1987); at that time, therefore, more timber was dying than was being cut. These mortality data represent an annual death rate of 1.36% of the total inventory and 69% of the annual growth of growing stock. These rates are quite high in comparison to the mortality rate (0.9%) in Illinois in 1962 and to rates in neighboring states—central Wisconsin, for example, had an average mortality rate of only 0.8% of its total inventory in 1983 (Raile and Leatherberry 1988). The Illinois secondary forests are aging, with concomitant increasing mortality. Disease accounted for 38% of the mortality, but weather, suppression, and unknown causes were also important (Hahn 1987). Elms suffered the greatest mortality and accounted for 26% of total mortality; 56% of the elm mortality was due to disease.

Ownership

Over 90% (3.64 million acres) of the commercial forests in Illinois are privately owned, mostly by farmers (45.3%) and other individuals (38.1%) (Figure 10). The remaining 10% is publicly owned, primarily by the federal government (7.2%) in the form of the Shawnee National Forest. The Cooperative Extension Service of the U.S. Department of Agriculture estimated that Illinois had 169,073 private

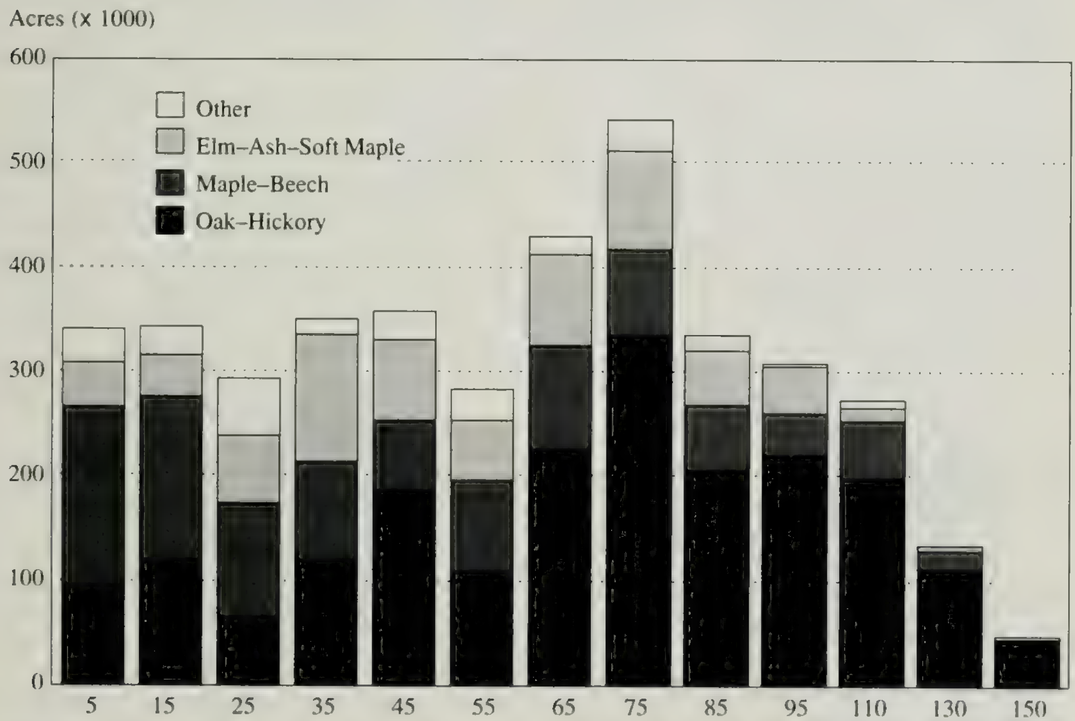

Figure 9. Acreage by age classes (in years) of the three major forest types in Illinois in 1985. Source: Hahn 1987.

forestland owners, each of whom owned an average of 21.5 acres of forest. The primary reasons for forest ownership given by the holders of small parcels were wildlife habitat and aesthetic value (Young et al. 1984); income was of greater importance for those who owned large forest parcels (McCurdy and Mercker 1986).

BENEFITS OF ILLINOIS FORESTS

Although Illinoisans would undoubtedly respond in different ways if queried on the benefits of the forests of our state, probably none of them would be in error. The forests of Illinois truly offer multiple benefits and perhaps one of the most encouraging aspects of management is that plans can be designed to accommodate and enhance these varied benefits.

Natural Communities

In the late 1970s, a search for natural communities relatively undisturbed by human activity was undertaken throughout the state (White 1978). Of the 1,089 natural areas selected for inclusion in the Natural Areas Inventory, 392 (36%) contained forestland; however, only 149 natural areas, a mere 11,593 acres of forestland, were classified as Grade A (relatively undisturbed) or Grade B (some disturbance). Of that total, about a third was classified as Grade A. Since that inventory, a few additional high-quality sites have been added, for a total of 157 areas from 62 counties. Lake and St. Clair counties contain the largest number of forested natural areas (12 and 11, respectively); Peoria has 7, Washington and Mason 6 each, and Massac 5. Adams County has the most extensive acreage of high-quality forestland, 1,950 acres, followed by St. Clair (963 acres), Lake (635 acres), Johnson (622 acres), McLean (450 acres), Saline (447 acres), Cook (444 acres), and Pike (431 acres).

Many high-quality forests in Illinois are undergoing degradation because of the invasion of exotic plants. Over much of the state, forests are threatened by garlic mustard (*Alliaria petiolata*), Amur honeysuckle (*Lonicera maackii*), tatarian honeysuckle (*L. tatarica*), Japanese honeysuckle (*L. japonicus*), multiflora rose (*Rosa multiflora*), autumn olive (*Elaeagnus umbellata*), and other introduced species. These exotics reduce the diversity of forest communities by eliminating native understory species. Management strategies must be adopted within the few remaining high-quality forests if they are to be protected from aggressive species. Control measures include recruiting volunteers for hand weeding, the cautious application of pesticides, and the implementation of biological controls. Perhaps most important is an educational program to teach the public how to identify and control these dangerous invaders.

Botanical Diversity

Illinois forests provide habitat for an exceptional diversity of plant species and are the natural home for most trees and other woody species. The 508 taxa of trees, shrubs, and lianas found in Illinois represent 15.9% of the state's reported flora, and 346 (69%) of them are associated with forest habitats (ILPIN data: Iverson and Ketzner 1988) (Figure 11). Most of the remaining taxa are cultural (escaped from cultivation). Of the 508 taxa, 370 (73%) are native to Illinois; the remaining are introduced. A relatively high proportion of the state's woody taxa are listed as rare in Illinois (40%); 15% occur commonly, 33% occur occasionally (common in localized patches), and 12% are

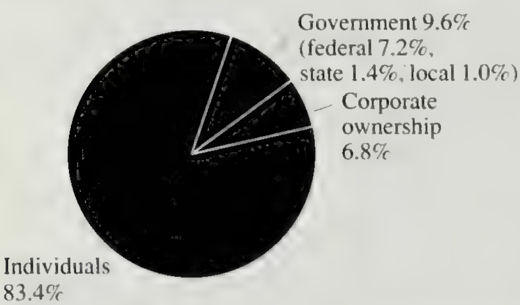

Figure 10. Ownership of Illinois commercial forests, 1985. Source: Hahn 1987.

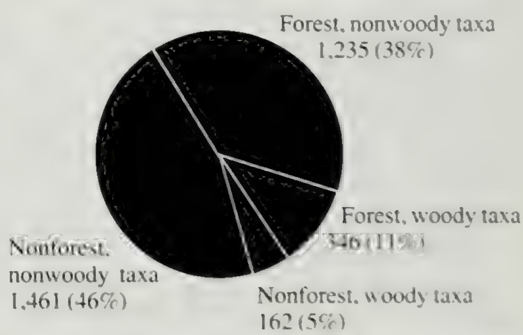

Figure 11. Number of plant taxa by habitat and habit (woody and nonwoody). Total taxa in Illinois = 3,204. Source: Iverson and Ketzner 1988.

uncommon (localized distribution or sparse throughout).

Illinois forests also provide habitat for an amazing number of nonwoody taxa. Including the woody taxa, fully 1,414 native taxa (61% of the native Illinois flora) are associated with forest habitats (Figure 11). Thus Illinois forests, which occupy only 12% of the area of the state, provide habitat for over half of its native flora. If we are to protect this irreplaceable biological diversity, we must maintain and restore forest communities. Beyond the importance of forestland as habitat for total plant diversity, rare plant species are frequently found in forest habitat, for example, 166 taxa (47%) of the 356 plants listed as threatened or endangered in Illinois are forest inhabitants. The importance of high-quality forests as refuges for these taxa cannot be overemphasized, especially in the face of extreme pressures from urban and agricultural growth.

Wildlife Habitat

Illinois forests provide the major habitat for numerous wildlife species, and losses in the quality and quantity of that habitat severely affect wildlife populations (Illinois Wildlife Habitat Commission 1985). Game species—gray squirrel, eastern wild turkey, quail, and white-tailed deer—depend on woodlands as do many more nongame animals—thrushes, warblers, woodpeckers, nuthatches, kinglets, and whippoorwills—to mention only a few bird species. But some relationships between wildlife and forests are more subtle. Most of us recognize the dependence of wood ducks on natural cavities in the trees of bottomland forests, but bottomland forests also provide food and habitat for fish, mitigate the effects of floods, restrain the movement of harmful chemicals into lakes and streams, and provide shade, thereby lowering water temperatures during stressful summer months.

One method of summarizing the value of Illinois wildlife habitat is based on land use. Complete details are presented in Graber and Graber (1976), and revised calculations based on current data are given in Iverson et al. (1989). The habitat evaluation index devised by Graber and Graber is based on the relative amount of a particular habitat type within a given area, the availability of that habitat type within the state or region, the changing availability of that habitat (Is it increasing or decreasing over time?), and the "cost" of a given habitat measured in years required to replace the ecosystem. A summary of habitat factors for Illinois as a whole is presented in Table 3. By this calculation, over three-quarters of the wildlife habitat (88 of 115.7 habitat factor points) is derived from forests. Elm–ash–cottonwood rates highest because this forest type has been disappearing so quickly over the past two decades (Figure 6). Oak–hickory values would be higher except that numbers in older age classes are increasing as secondary forests mature, even though numbers in younger age classes are decreasing (Figure 9). A very minor rating was earned by maple–beech because this forest type has increased so dramatically in recent years (Figure 6).

This method can be used to evaluate wildlife habitat on parcels of various size (see examples in Iverson et al. 1989). In the final calculation, the habitat factor for a given site or region is divided by a regional or statewide habitat factor (115.7 for the state). An index of 1.0, therefore, means that the value of the habitat under consideration is about average for the state or region as a whole. Thus, a habitat evaluation index of 1.5, the value calculated for the 16 southern counties, indicates a much higher wildlife value than the value of the state overall. Similarly, the value of 0.66 for the 60 northern counties indicates a relatively poor

Table 3. Habitat factors for Illinois, 1985, calculated according to Graber and Graber (1976).

Land type	Habitat factor	Percent of habitat factor
Forest		
Pine	5.70	4.9
Oak–hickory	30.07	26.0
Oak–gum–cypress	11.97	10.3
Elm–ash–cottonwood	40.19	34.7
Maple–beech	0.14	0.1
Subtotal		76.0
Nonforest		
Cropland	0.29	0.3
Pasture/hayland	10.01	8.7
Prairie	1.46	1.3
Marsh	15.28	13.2
Water	0.38	0.3
Urban, residential	0.03	0.0
Fallow	0.19	0.2
Subtotal		24.0
Total	115.73	100.0

habitat for wildlife, and the value of 1.09 for the 26 south-central counties indicates wildlife habitat somewhat above that of the state as a whole.

Fragmentation of forest habitat has negative implications for wildlife, especially for neotropical migrant birds that need large blocks of uninterrupted forest for successful nesting (Harris 1984; Blake and Karr 1987; Robinson 1988). As large tracts of forest are broken into small, isolated woodlots, more forest edge is created and more opportunities exist for edge-adapted species, most importantly the cowbird, to invade the area and parasitize the nests of many forest songbirds.

The extent of fragmentation in Illinois forests was made clear in a recent examination of forest parcels by size. Relying on the Illinois Geographic Information System and data from the U.S. Geological Survey, researchers determined that 10,121 forested parcels exist in the state and that the average size per parcel is 358 acres (Iverson et al. 1989). About 44% of the parcels are less than 100 acres in size and about 10% are larger than 600 acres (Figure 12). Perhaps the density of forest parcels can be pictured more clearly if we envision an area the size of a township—36 square miles. On average, 6.1 parcels exist per township-sized area, with 69% of them roughly 40 (limit of resolution of the data) to 200 acres in size. This perspective makes clear that Illinois forests are extremely fragmented and that a concentrated effort must be made to protect larger forest patches and to aggregate smaller ones.

Figure 12. Number of forested parcels in Illinois by size and average number of parcels per township equivalent (36 square miles). Total number of parcels in Illinois of a given size is the number immediately following the size (e.g., <100-acre parcel: 4,479). Average number of parcels of a given size per township equivalent is given in parentheses. Source: Iverson et al. 1989.

Soil and Water Quality Protection

Soil erosion with its accompanying degradation of surface water is indeed a serious threat to the future of an agricultural state: for every pound of corn, soybeans, wheat, or oats grown in Illinois, 3.3 pounds of soil are lost (Iverson et al. 1989). In contrast to cropland, forest vegetation protects against excessive soil loss. Average erosion of cropland proceeds at about four times the annual rate of nongrazed forestland—7 tons per acre compared to 1.6 tons, respectively. The difference in soil loss is even greater on sloping, highly erodible soils. Soils with land capability ratings of IVe to VIIe lose 24.2 to 39.4 more tons per acre each year they are under cultivation than they would lose if they were forested. In 1982, 1.75 million acres of cropland had these capability ratings. Had those acres been converted to nongrazed forestland, 36.5 million of the 157.8 million tons of soil lost annually from cropland would have been saved. Figure 13 shows that the soil savings that would result from converting cropland with higher capability ratings to nongrazed forest would be disproportionately higher than conversions from cropland with lower ratings.

The Conservation Reserve Program is designed to remove marginal cropland from cultivation, and it is helping; however, over 96% of the cropland currently being removed from production in Illinois is going into grass rather than trees. The U.S. Department of Agriculture and the Illinois Council on Forestry Development are working together to alter this percentage in favor of trees.

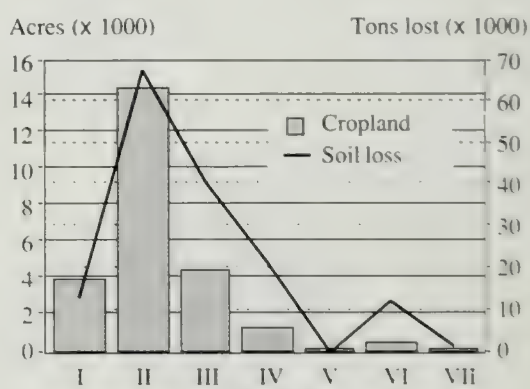

Figure 13. Cropland acreage and annual soil loss by capability class. Class I soils are most productive; Class VII soils are least productive. Source: U.S. Soil Conservation Service data base 1982.

Heavy grazing, and especially feedlot operations, in forestlands largely negates the benefits of soil protection. Average soil loss from forestland that is heavily grazed or under feedlot operations is 13.1 tons per acre per year in contrast to only 1.6 tons per acre per year on nongrazed forest. Thus, 66% of the 12.6 million tons of soil lost annually from forestland is lost from these areas, even though only 19% of Illinois forests are categorized as grazed. Light grazing of forestland generally does not increase soil loss significantly and is certainly to be preferred over cultivation of marginal lands.

According to estimates by the U.S. Forest Service, 133,100 acres of windbreaks existed in Illinois in 1985 (Hahn 1987). Windbreaks retard soil loss due to wind erosion, but they also provide shade for livestock and shelter for wildlife. Their aesthetic qualities are not to be overlooked, but their role in the conservation of energy is growing in importance. Back in 1981, the Soil Conservation Service estimated that 124,000 buildings in rural Illinois needed windbreaks. Had they been planted, energy equivalent to 941 million kilowatt-hours of electricity could have been saved (USDA Soil Conservation Service 1982).

Recreation and Scenic Values

In 1987, surveys by the Illinois Department of Conservation indicated that Illinoisans spent about 240 million days or portions of days pursuing recreation on or near forestlands; in the process they spent approximately $6.3 billion (Illinois Department of Conservation 1989). Activities closely aligned with forest recreation (picnicking, observing nature, cross-country skiing, backpacking, hiking, camping, canoeing, horseback riding, snowmobiling, riding off-road vehicles, trapping, and hunting) accounted for 206 million of those days, an average of 18.7 days per resident (Figure 14).

The majority (93%) of the 4,528 areas developed for recreation in Illinois (almost 900,000 acres) are publicly owned and operated. Total land available for recreation totals roughly 2.7% of the state's land and water area, a per capita outdoor recreation acreage of less than 0.1 acre. Among states, Illinois rates 46th in total public open space per capita. In addition, most of the publicly owned land available for recreation is located in the southern part of the state; the majority of Illinoisans, however, live in the north.

Urban Forests

Most Illinoisans (83%) live in urban centers, and urban forests are often their only exposure to a natural environment. Urban forests provide many benefits beyond those normally associated with rural forests, including temperature modification and energy conservation; the abatement of air, water, and noise pollution; the masking of unpleasing urban views; and physical and psychological benefits to city dwellers. Because the urban forest exists in such a heterogeneous environment, an accurate assessment of its extent and function is difficult. The U.S. Forest Service, however, has estimated that 102,800 acres of urban forest and 139,500 acres of urban areas with trees existed in Illinois in 1985 (Hahn 1987). Cook County alone has over 67,000 acres of forest preserves, and much of this land is available for recreation. A recent remote-sensing study revealed that 21.3% of the land area in the six-county Chicago area had tree cover in 1988 (Cook and Iverson 1991). Yet less than 0.01 acre per capita of publicly owned forestland exists in that six-county area, and Chicago ranks last among the nation's ten largest urban centers in this regard.

Urban forests face three problems. First, maintenance and management are inadequate. A recent survey by the Illinois Council on Forestry Development (1988) estimated that 6.5 million municipal street trees exist in Illinois with an estimated value of $3 billion. These trees are generally not adequately maintained because of inadequate budgets and the lack of trained foresters. In addition, less than half the potential number of street trees are presently in place, and removals outstrip plantings (American Forestry Association 1988). Second, forestlands are jeopardized by

Figure 14. Days (in thousands) spent in recreational pursuits on or near forestlands in Illinois, 1987. Source: Illinois Department of Conservation 1989.

development and population pressures. Tremendous growth is now occurring in the six collar counties around Chicago. Information from the Northeastern Illinois Planning Commission (1987) shows that 867 quarter sections (about 5.6% of the area) were urbanized (population density exceeding 1,000 per square mile) between 1970 and 1980. Much of this growth was at the expense of forestland. A third problem is the absence of a policy for using wood waste. Until recently, much of the debris from tree removals and large amounts of other wood wastes were deposited in landfills, an enormous waste of wood and leaf mulch and the needless use of costly landfill space. Better uses for this material must be developed and marketed.

Timber Products

Illinois ranks fifth in the nation in demand for wood but 32nd in production. As a result, Illinois imports much of the wood it uses from neighboring states. In addition, 14.2% of the wood harvested in Illinois is processed in neighboring states and then often imported back into the state. Currently, the annual growth of timber (96 million cubic feet) exceeds timber removals (68.6 million cubic feet removed for timber products, logging residues, and changing land uses), and a higher proportion of the state's demand for wood could be met within its own boundaries if the processing facilities were at hand. With judicious management, harvesting could be increased, negative effects on the environment minimized, and multiple benefits achieved.

In 1983, 161 million board feet of timber (mbf) were harvested in Illinois (Blyth et al. 1987); 146 mbf were processed in 178 Illinois sawmills. Red oak (29%), pin oak (19%), white oak (16%), and cottonwood (10%) accounted for the majority of sawlogs processed in the state. Of the 4 mbf of veneer and other high-quality logs (mostly white oak, walnut, and red oak) cut in Illinois during 1983, only 0.3% remained in the state. Additionally, all pulpwood (7.2 million cubic feet) produced in the state were processed elsewhere. The veneer and pulpwood statistics are not surprising because virtually no plants for either veneer or pulpwood are found in Illinois.

An enormous quantity of fuelwood is harvested from Illinois woodlands. In 1982, nearly 2 million cords of firewood were cut or gathered, a figure that represents 43% of the total trees utilized that year! The major harvest of fuelwood takes place in the heavily populated northeastern counties. Cook, McHenry, and Will counties, for example, each harvested over 150,000 cords of fuelwood in 1983 (Blyth et al. 1985). The majority of firewood (97%) was cut from private lands, and 75% was gleaned from dead trees.

According to U.S. Department of Commerce figures, forest-related industries in Illinois employ 55,000 people with an average payroll of $965 million. These firms contribute more than $2 billion annually to the state's economy through value added by manufacture; in addition, they invest more than $144 million in capital improvements annually (U.S. Department of Commerce 1982–1985).

According to 1984 data from Dun & Bradstreet, 166,900 employees work for 957 Illinois firms that are primarily involved in the manufacture of wood products. If the paper industry is included, an additional 576 firms and 367,450 persons are involved (Figure 15). The Dun & Bradstreet numbers are much higher than those released by the U.S. Department of Commerce because Dun & Bradstreet include the total number of employees, even those not directly associated with the wood-manufacturing component. Nonetheless, a large number of employees work in forest-related industries, most of which are located in the Chicago region.

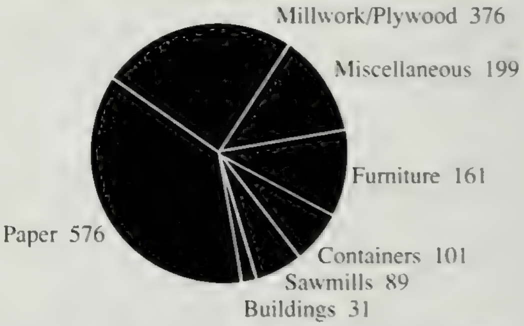

Figure 15. Forest-related industries in Illinois, 1984. These 1,533 sites employed 534,342 workers. Source: Dun & Bradstreet data base 1984.

CONCLUSIONS

A great deal of information has been presented to establish the initial contention of this paper: the Illinois forests provide numerous important benefits to the citizens of the state. Nevertheless, considerable improvement in the quantity and quality of these benefits could be achieved if forestlands were better managed. Over most of the state, little forest management is underway, and the potential of our forests to provide wildlife habitat, preserve biodiversity, and extend wood production has not been tapped. Even in "wilderness" areas, management is often necessary to maintain the status quo (e.g., remove exotic invaders). Ecosystems are not static entities; change is inevitable, but only with management can change benefit the resource as well at its human guardians.

We need to manage the forest resources we currently possess, but we also need to plant more forests if we are to assure continuing benefits from our forests. Recent political developments have and may continue to support tree planting programs; however, caution is in order. Planting trees requires more than seedlings and a spade. Species most appropriate to a given site must be selected, follow-up care must be available, and long-term management must be provided if the success of these programs is to be ensured.

The environmental problems facing Illinois, the nation, and the planet are grave indeed. Yet we are learning the important role that forests can play in mitigating some of these problems. We have, however, only begun to realize the enormity of the task. We have only begun to take the actions needed to create a sustainable world.

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Forest Succession in the Prairie Peninsula of Illinois

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Presently most of central Illinois is in the Grand Prairie Natural Division (Schwegman 1973), classified as a part of the prairie peninsula of the oak–hickory forest region by Braun (1950), as a mosaic of bluestem prairie and oak–hickory forest by Küchler (1964), and as a part of the prairie–deciduous forest ecotone by Davis (1977). At the time of settlement by Europeans, prairie dominated most of Illinois. Forests were common, however, occurring on rough terrain such as moraines and dissected valleys of streams and rivers and as isolated groves on the flat to gently rolling prairie.

During postglacial times, the vegetation of Illinois changed extensively (King 1981). Pollen diagrams from the prairie peninsula in Illinois record the climatically related vegetation shifts that have occurred since the late Pleistocene. The pollen record for Chatsworth Bog, Livingston County, in the center of the prairie peninsula, suggests that a mosaic of open spruce woodlands and tundra existed there from 14700 to 13800 BP. This cover type in turn was replaced by an ash/tundra assemblage that reflected the slowly increasing temperatures of the late-glacial from 13800 to 11600 BP. After 11600 BP, pollen from deciduous trees and shrubs increased dramatically, starting with cool-climate species (birch, hazel, black ash) and followed by such warm-tolerant taxa as elms, oaks, and hickories. By 8300 BP, prairie dominated the area as indicated by a dramatic decrease in tree pollen and a corresponding increase in the amount of pollen from herbaceous plants. Oak pollen was still present, however, suggesting that prairie vegetation was probably common on the drier flat uplands while the lowlands and river valleys retained their forest cover. These open expanses of prairie with savanna and forest communities restricted to the more dissected lands were what the early European settlers found when they entered the prairie peninsula of Illinois in the early 1800s.

The presettlement distribution of the major vegetation types in Illinois (prairie, savanna, and forest) was determined largely by firebreaks such as lakes and rivers and by topographic relief that controlled the frequency and intensity of fire (Gleason 1913; Wells 1970; Grimm 1984). Gleason (1913) found that forests were more extensive on the east side of firebreaks, while prairie tended to be more extensive on the west side. This distribution pattern was the result of prevailing westerly winds that carried fires to the western sides of firebreaks, thus encouraging the development of prairies. In contrast, the eastern sides were protected from fires, and forest developed at these locations.

PRESETTLEMENT FORESTS

In presettlement times, according to survey records of the General Land Office, prairie occupied 61.2% of Illinois and forest and savanna accounted for 38.2% (Iverson et al. 1989). In general, prairie vegetation was most common on flat to gently sloping ground; savanna and forest were most common in dissected areas. The segregation of forest, savanna, and prairie on the basis of topography apparently occurred because dissected landscapes do not readily carry fire. For the most part, these dissected landscapes have well-developed drainage systems that support permanent or temporary streams, which serve as firebreaks. In addition, fires in hilly areas tend to move up slope relatively rapidly due to rising convection air currents, but convection currents work against fires when they move down hill, not uncommonly causing them to burn themselves out.

A great deal of vegetation information can be obtained from survey records of the General Land Office (Bourdo 1956). The job of the surveyors was to establish a grid system of township, range, and section lines by the

placement of section and quarter section corner posts. In prairie and marsh areas, only posts were used. In timbered areas, however, two (or four) witness trees were blazed, and the distance and direction of these trees from the corner posts were recorded along with their species and estimated diameter at breast height (dbh). Because the placement of the corner posts and the selection of witness trees were essentially random, the principles of the distance method (Cottam and Curtis 1956) can be applied to the witness tree data and the composition and tree density of the presettlement savannas and forests determined.

In Illinois, several researchers have used survey records of the General Land Office to determine the extent, composition and densities of tree species for various counties. Some of their studies are summarized here and indicate the extent and composition of the presettlement vegetation of the prairie peninsula.

Kilburn (1959) found that the original forest in Kane County consisted largely of oak openings composed of pure bur oak or bur/white oak stands. Lowlands and swamp forests were found along rivers and streams, but a more mesic forest occurred on the heavier soils of the Big Woods area. Overall, three-fifths of the county was prairie. Topography accounted for most of the vegetation pattern: level areas were in prairie vegetation; protected ravines, valleys, steep bluffs, and hills were largely forested. Overall, 87% of the witness trees recorded by the surveyors were oaks and hickories.

In Lake County, the situation was similar. Oak and hickory species accounted for 95% of the trees recorded (Moran 1976). In this county, however, savanna was the dominant vegetation type, occupying 51% of the area. It was found mostly on rolling uplands that were frequently broken by small wetlands or streams; bur oak was by far the most common species with black and white oaks in lesser numbers. Prairie, wet prairie, and marsh occupied 33% of the county while forests occurred in the remaining 16%. For the most part, prairies were situated on flat terrain and forests were restricted to areas of rough topography or where natural firebreaks afforded some protection.

In McLean County, located in west-central Illinois, the presettlement vegetation was 89.5% prairie, 5.4% savanna, 1.8% open forest, and 3.3% closed forest (Rodgers and Anderson 1979). The forested areas occurred on the more rugged topography associated with rivers, streams, and glacial moraines. White and black oaks were the most numerous species recorded, but in the closed forests (273 trees/ha) the more mesic species (i.e., sugar maple, elm, red oak, buckeye) accounted for about one-third of the trees present. These more shade-tolerant, mesic species, which for the most part are fire-sensitive, occupied sheltered ravines and areas adjacent to streams where fires occurred infrequently. In contrast, the relatively shade-intolerant oaks, which depend on periodic fires to maintain their dominance, were more common on less dissected uplands.

In adjacent Mason County, similar results were obtained (Rodgers and Anderson 1979). Located in the Illinois River Sand Area Section (Schwegman 1973), on soils developed from deep sand deposits laid down by glacial meltwater during the Pleistocene (Willman and Frye 1970), prairie was the dominant vegetation type, occupying 67.7% of the county. Savanna (14.4%) and forest (13.3%) occurred on most of the remaining land and 4.6% was covered by lakes and swamps. The dominant tree species in the presettlement forests and savannas were shade-intolerant, fire-tolerant black and blackjack oaks. In the closed forests (263 trees/ha), the oaks and hickories were still the most numerous species. The more mesic, shade-tolerant, fire-sensitive tree species (i.e., sugar maple, elm, walnut) were also found in the closed forests, particularly in areas of rough topography.

In Douglas County, near the southern edge of the Grand Prairie Natural Division (Schwegman 1973), prairie was the most widespread plant community (85%). Closed forest, which was generally restricted to the major river systems, accounted for the remaining 15%. These forests were dominated by white and black oaks and hickories, species that accounted for 70% of the witness trees recorded by the surveyors. Mesic, shade-tolerant, fire-sensitive species were present but restricted to areas of rough topography and river valleys (Ebinger 1986a).

Prairie was the most widespread vegetation type (60%) in Coles County, the southern half of which is located on the Shelbyville Moraine, the terminal moraine of Wisconsin glaciation. Prairie was most common on the flat to gently rolling uplands in the northern and

central parts of the county. Forests, which accounted for most of the remaining 40%, were restricted to the rough topography of the terminal moraine and to the valleys of the Kaskaskia and Embarras rivers. More than 80% of the witness trees recorded were oaks and hickories, with white, black, and red oaks most numerous. Again, more mesic species were restricted to rough topography (Ebinger 1987).

Information extrapolated from the records of early surveyors indicates that prairie vegetation dominated most of Illinois in presettlement times and was found on the flat to gently rolling uplands throughout most of the state. Savannas and forests, in contrast, were more common in rough topography, especially in the driftless areas, along major waterways, and where morainal systems provided topographic relief. For the most part, savannas developed on sites where the frequency of fire was reduced, thereby permitting the establishment of fire-tolerant tree species (Anderson 1970; Anderson and Anderson 1975; Grimm 1984; Anderson and Brown 1986). Forests, particularly closed forests, developed in places of rough relief, in river valleys, and in other protected areas where fires were less likely to occur. Oaks and occasionally hickories dominated the open savannas. In the forests, oaks and hickories were also the dominant species, but more mesic, shade-tolerant, fire-sensitive tree species were common forest components. Furthermore, the transition from forest to prairie varied from being rather abrupt in some locations in the prairie peninsula to others where savannas formed a broad transition between forest and prairie (Nuzzo 1986). This transition was probably determined by topographic relief, firebreaks, fuel loads, and other edaphic and climatic factors that controlled the frequency and intensity of fires.

PRESENT SUCCESSION TRENDS

During the past century and a half of agricultural development, periodic fires have ceased in the prairie peninsula, and the oak savannas and open oak forests on the uplands have become closed-canopy forests. As a result, these woodlots have been changing to forests dominated by such mesic, shade-tolerant, fire-sensitive species as sugar maple, American and red elms, white and green ashes, and ironwood (Anderson and Adams 1978; Adams and Anderson 1980; Ebinger 1986b).

In particular, sugar maple has increased in importance in most Illinois forests (Iverson et al. 1989). If this trend continues, many of the oak–hickory forests, their understories, and the wildlife that depends upon them will be in serious trouble in the near future. Even the best quality oak–hickory communities are apparently undergoing an irreversible change as sugar maple and other mesic, shade-tolerant species replace many of the original forest components. Almost no work has been done concerning methods to reverse this trend, and the problem now concerns many ecologists and managers of natural areas.

Many of the better quality forests that presently exist in the prairie peninsula have been surveyed during the past thirty years. In a few of them, sugar maple is not an important component, though other mesic species are sometimes common. At Walnut Point State Park in Douglas County (Ebinger et al. 1977), sugar maple is rarely encountered, and oaks and hickories are by far the most numerous species. In the forests and savannas of the Kankakee Sand Area Section (McDowell et al. 1983) and the Illinois River Sand Area Section (Rodgers and Anderson 1979) oaks dominate and mesic species are rarely encountered. In most of the stands studied, however, mesic species, particularly sugar maple, are relatively important components. These mesic species are also well represented in the seedling and sapling categories and in the smaller diameter classes. Oaks and hickories, in contrast, are poorly represented in these categories.

Mesic, shade-tolerant, fire-sensitive species are common components of many recently surveyed forests in the prairie peninsula. Two "prairie grove forests" in Champaign County have been surveyed at various times in the past, and sugar maple is an important component in both. In Trelease Woods (Boggess 1964; Pelz and Rolfe 1977), sugar maple dominates the seedling and sapling categories as well as most of the diameter classes. Similar results were obtained for Brownfield Woods by Boggess and Bailey (1964) and Miceli et al. (1977).

An inventory of the woody vegetation of Funks Forest Natural Area in McLean County was conducted by Boggess and Geis (1966). This forest is an example of a mesophytic forest that is transitional between the upland oak–hickory cover type and the "prairie grove

forest." Sugar maple, the dominant species in Funks Forest, is followed closely by white oak and elm. Sugar maple and white oak, however, represent two distinct age classes. White oak, which predominates in the 30-inch-diameter class, is a "pioneer" species; and sugar maple, which predominates in the 16-inch-diameter class, has perhaps been increasing steadily in importance during the past century.

One recently documented example of the increase in importance of sugar maple is at Baber Woods Nature Preserve in Edgar County. This 16-ha forest is located on the flat to gently rolling ground just north of the Shelbyville Moraine, the terminal moraine of Wisconsin glaciation. Two decades ago, McClain and Ebinger (1968) reported that sugar maple ranked second in importance in the woods and dominated the seedling, sapling, and smaller diameter classes. In a more recent survey of the same area, Newman and Ebinger (1985) found that this trend had continued. Sugar maple was now first in importance, and the number per acre had almost doubled. Further, sugar maple continued to dominate the seedling and sapling categories and accounted for nearly half of the individuals in smaller diameter classes. Sugar maple and oaks represent two distinct age classes in Baber Woods, as shown in Figure 1. These curves show that oaks predominate the larger diameter classes and suggest that these species have been an important forest component for an extended period of time. Sugar maple, in contrast, predominates the smaller diameter classes and has probably been increasing steadily during the past century. The large number of sugar maple seedlings, saplings, and smaller diameter trees suggests a continuation of this trend.

Table 1 indicates when sugar maples began to increase in importance in Baber Woods. In nearly every quadrat, sugar maple increased in number, size, and importance from 1965 to 1983. In addition, the number, size, and importance of sugar maple decreased from the northwestern corner of the woods, becoming smaller and less common toward the southeastern corner. This pattern suggests that sugar maple probably occurred in the ravines that exist just to the north and west of the woods, where in presettlement times it was probably protected from fire due to the rough topography. With the cessation of fire, this fire-sensitive species has been able to invade the upland forests that still exist in the area.

Another indication of the increase of sugar maple in Baber Woods is the distribution of this species and the oak species by diameter classes for the 1965 and 1983 surveys (Table 2). Sugar maple increased in all diameter classes between 1965 and 1983, particularly in two diameter classes, 10–19 and 20–29 cm. Sugar maple showed an overall increase of nearly 30 trees per hectare between the two surveys. In contrast, oak species decreased in numbers, dramatically so in the lower diameter classes, with increases occurring only in classes 60–69 cm in diameter and above (Table 2). Overall, species density increased in the woodlot, from 258.6 stems/ha in 1965 to 277.3 stems/ha in 1983. Most of this increase is due to sugar maple and other mesic species that are tolerant of shade and sensitive to fire. Presently the oaks are common in the larger diameter classes because of recruitment from the smaller diameter classes. Oak reproduction is sparse (McClain and Ebinger 1968; Newman and Ebinger 1985), and as the veteran trees die, fewer oaks are available to fill the canopy gaps. In contrast, sugar maple, with its high gap-

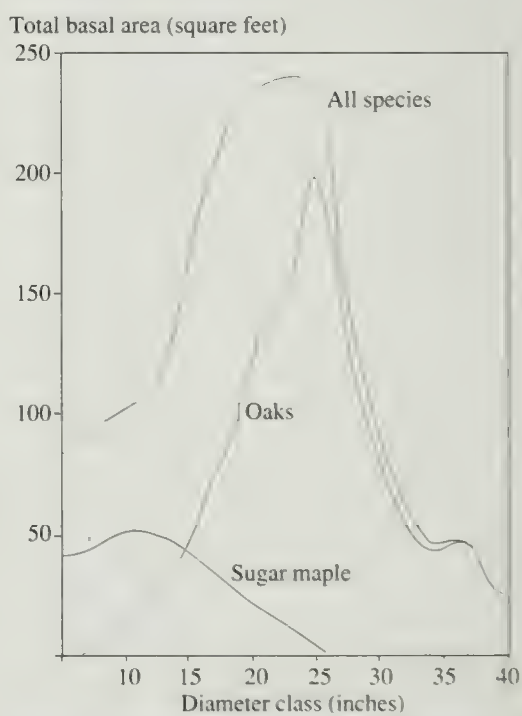

Figure 1. Smooth curves of basal area by diameter class for sugar maple, all oak species combined, and all species combined at Baber Woods, Edgar County, Illinois. Source: Ebinger 1986b.

phase replacement potential, is able to take advantage of these canopy openings (Ebinger 1986).

Within Baber Woods are a number of large open-grown white oaks. In a walk-through survey conducted during the early spring of 1990, twenty-six large, open-grown white oaks were observed. All have open, round crowns and large lower branches, some within 4 m of the ground. They are probably remnants from a time when this forest was an open, upland savanna. The average diameter of these open-grown white oaks is 101.6 cm dbh, and two that had died recently were cut and aged at 313 years. Both had fire scars at 65 and 77 years, indicating that in the past fires were probably common in the area. Five other oaks that had died recently were also cut and aged.

Table 1. Distribution of sugar maple in Baber Woods Nature Preserve, Edgar County, Illinois, for the surveys of 1965 (McClain and Ebinger 1968) and 1983 (Newman and Ebinger 1985). The following information is given for each quadrat (1 ha): the number of stems present (above 10 cm dbh), the number of stems exceeding 40 cm dbh, the average diameter (cm), and the importance value (relative density and relative dominance) for sugar maple. Highest possible importance value is 200. The northern edge of the woods is represented in quadrats 1 through 4.

	Quadrat 1		Quadrat 2		Quadrat 3		Quadrat 4	
	1965	1983	1965	1983	1965	1983	1965	1983
Number of individuals	140	153	158	152	104	124	82	102
Number <40 cm dbh	8	14	12	17	3	4	2	9
Average diameter (cm)	23.1	23.6	22.1	25.3	19.3	20.9	20.1	22.7
Importance value	78.1	86.2	82.4	98.6	52.6	68.1	42.1	57.5

	Quadrat 5		Quadrat 6		Quadrat 7		Quadrat 8	
	1965	1983	1965	1983	1965	1983	1965	1983
Number of individuals	98	134	91	138	90	100	45	70
Number <40 cm dbh	7	9	5	6	3	6	1	4
Average diameter (cm)	20.6	20.5	19.1	19.4	18.9	21.6	19.5	20.4
Importance value	51.2	71.9	45.9	66.7	45.8	58.3	25.1	37.8

	Quadrat 9		Quadrat 10		Quadrat 11		Quadrat 12	
	1965	1983	1965	1983	1965	1983	1965	1983
Number of individuals	60	95	29	101	38	74	34	58
Number <40 cm dbh	9	14	—	1	—	2	—	1
Average diameter (cm)	23.5	21.1	15.6	15.5	19.8	20.2	18.5	20.9
Importance value	40.8	53.2	13.8	39.2	25.4	45.8	20.4	34.5

Table 2. Density (number/ha) in broad diameter classes for sugar maple, oak species, and all other species in Baber Woods Nature Preserve, Edgar County, Illinois, for the surveys of 1965 (McClain and Ebinger 1968) and 1983 (Newman and Ebinger 1985).

	Sugar maple		Oak species		Other species		Totals	
Diameter class	1965	1983	1965	1983	1965	1983	1965	1983
10–19 cm	42.6	58.9	7.6	3.7	50.0	62.1	100.2	124.7
20–29 cm	17.8	24.7	10.9	4.9	17.0	17.7	45.7	47.3
30–39 cm	7.3	10.6	14.7	8.3	19.0	13.2	41.0	32.1
40–49 cm	2.4	4.6	17.7	11.6	15.4	12.6	35.5	28.8
50–59 cm	0.6	1.0	16.2	13.0	5.6	7.9	22.4	21.9
60–69 cm	0.1	0.3	7.5	11.1	0.9	2.1	8.5	13.5
70–79 cm	–	–	2.7	4.4	0.3	0.6	3.0	5.0
80–89 cm	–	–	1.1	2.3	0.1	0.2	1.2	2.5
90+ cm	–	–	1.1	1.5	–	–	1.1	1.5
Total	70.8	100.1	79.5	60.8	108.3	116.4	258.6	277.3

These were forest-grown trees with straight trunks, no low branches, and an average diameter of 68.2 cm. They varied in age from 140 to 158 years, with an average age of 148 years. In contrast were the increment cores obtained from 30 sugar maples in various parts of the woodlot. Those from the northwestern part of the woods, where the largest individuals occurred, averaged 44.7 cm dbh and had an average age of 107.6 years. Sugar maples from the northeastern and southeastern corners of the woodlot were smaller and younger (Table 3).

The data suggest that before European settlement, the area now known as Baber Woods was an open, white oak savanna maintained by periodic fires. This community was probably parklike with an understory of prairie grasses and forbs. With the cessation of fire, the number of seedlings increased and began to fill the gaps in the canopy between the large open-grown oaks. As shade increased, moisture levels within the forest probably increased, creating a habitat for more mesic, shade-tolerant, fire-sensitive species such as sugar maple.

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Table 3. Tree rings and diameters (dbh) of sugar maples at selected sites in Baber Woods Nature Preserve, Edgar County, Illinois.

	Diameter (cm)		Growth ring	
Area	Range	Average	Range	Average
Northwest corner	37.4–59.7	44.7	101–116	107.6
Northeast corner	26.0–35.8	30.4	52–91	70.6
Southeast corner	17.5–35.5	25.7	51–71	61.1

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Effects of Forest Fragmentation on Illinois Birds

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Abstract. The forests in Illinois are among the most fragmented in North America. Most remaining tracts are small, isolated, and dominated by "edge" habitats. Populations of many forest species, especially those that breed in the forest interior, have been declining, and many characteristic forest species do not occur in woodlots below a certain minimum size. Data from small woodlots (<65 ha; 170 acres) in the Lake Shelbyville area of central Illinois suggest that reproductive failure may be at least partly responsible for these trends, especially among the neotropical migrants that breed in Illinois but winter in the tropics. Most nests fail because of brood parasitism by brown-headed cowbirds (*Molothrus ater*) (76% of all nests of neotropical migrants) or because of nest predation (80% of all nests).

Brown-headed cowbirds, which are abundant throughout Illinois, pose a particularly severe threat because they lay their eggs in the nests of host species, which go on to raise cowbirds instead of their own young. Parasitized nests in the Lake Shelbyville area averaged 3.3 cowbird eggs per parasitized nest. All 19 wood thrush (*Hylocichla mustelina*) nests were parasitized with an average of 4.6 cowbird eggs per nest. Only about 10% of the birds of all species caught in midsummer were juveniles. These data strongly suggest that the reproduction of neotropical migrants in very small woodlots is insufficient to compensate for adult mortality, a result consistent with the population declines observed in the Shelbyville area.

Birds nesting in much larger tracts (up to 2,024 ha; 5,000 acres) in the Shawnee National Forest appear to face similar problems. A crew of 14 workers located over 400 nests in 1989 and discovered that cowbird parasitism and nest predation rates were high, even deep in the forest interior. In contrast to studies elsewhere, cowbirds were found throughout each study area, regardless of the proximity of edges. Over 55% of all nests were parasitized and an average of 60% of all nests were destroyed by predators. As in Shelbyville, wood thrushes suffered most from cowbirds: 90% of all nests parasitized and an average of 3.2 cowbird eggs per nest. Other species that suffered high (>70%) parasitism rates were the red-eyed vireo (*Vireo olivaceus*) and the scarlet (*Piranga olivacea*) and summer tanagers (*P. rubra*). A few species reproduced successfully in spite of the abundance of nest predators and cowbirds. Worm-eating (*Helmitheros vermivorus*) and Kentucky warblers (*Oporornis formosus*) hide their nests effectively, and for these species young outnumbered adults in midsummer samples of birds caught in mist nests.

These results suggest that management decisions will have to take into account differences among species in susceptibility to forest fragmentation. The cowbird situation is more serious than has been anticipated and apparently cannot be solved simply by minimizing edges as has been proposed elsewhere in the Midwest. At least a few species, for example, the wood thrush, may be in serious trouble throughout the Midwest and should receive special management attention.

Session Two: Prairies and Barrens

The chance to find a pasque-flower is a right as inalienable as free speech.—Aldo Leopold

The first Europeans to see the Illinois country had crossed a vast ocean, snaked their way through a nearly impenetrable mountain range, and forged a path through a thousand miles of dense, primeval forest. They did it with indomitable spirit and by sheer force of will. Yet when they reached the edge of the eastern deciduous forest, approximated today by the Indiana–Illinois border, they stopped in wonder. Here was a landscape so different from those with which they were familiar that they had no word for it. In time this landscape came to be known as "prairie," a word derived from the French word for *meadow*.

At first, early settlers avoided living on the prairie because the treeless grasslands were thought to be infertile. They did not provide much needed building materials, fuel, and water. Instead, they offered the prospect of menacing prairie fires and howling winter storms. Soon, however, the settlers realized that prairie made excellent cropland, especially after John Deere invented the moldboard plow that allowed virgin prairie soil to be broken. The wild prairies became cropland at an astonishing rate—approximately 3.3% per year. Over 300,000 people settled on the prairie during the decade of the 1830s, and by 1860 nearly all the prairies had disappeared.

At least 23 different kinds of prairies are found in Illinois—add barrens, savannas, and glades and the list increases to over 30. These various prairies once occupied nearly 22 million acres of the state. Today they are confined to about 3,000 acres, less than 0.01% of their original extent. Unfortunately, it is easier to find examples of the prairie's influence in the "prairie" state—Prairie Street, Prairie State Games, Prairie Farms Dairy, Prairieview Estates, Prairie Technology—than it is to find an actual prairie. Prairie remnants persist, however, along railroad lines, in pioneer cemeteries, even on the grounds of industrial complexes, growing in a forgotten corner of some storage yard yet to be developed.

Over 200 species of plants characteristically inhabit Illinois prairies. Although this number is relatively low compared with a typical undisturbed woodland, a small prairie remnant—as little as five acres—can be surprisingly diverse with more than 120 species of plants. All present-day Illinois prairies, however, are incomplete, fragmented ecosystems and lack the large herbivores that were so important in their development.

What if Illinoisans had had the foresight to preserve only 100 square miles of virgin prairie in central Illinois? What a tremendous natural resource and botanical laboratory that would be today! Inevitable though the destruction of the prairie may have been, it is truly unfortunate that prairies will be visualized by future generations as isolated pockets of native vegetation, persisting in a world that passed them by. Ironically, the French word for meadow, so incongruous when applied to this once vast grassland, now seems totally appropriate.

The session opened with a broad historical perspective of the tallgrass prairie. The papers that followed focused tightly on two aspects of that prairie—the remnant-restricted prairie and savanna insects of the Chicago region and the response of prairie birds to habitat fragmentation.

Illinois Prairies: A Historical Perspective

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The grasslands of central North America originated in the Miocene–Pliocene transition, about 7–5 million years before present (YRBP) and were associated with the beginning of a drying trend. The Miocene uplift of the Rocky Mountains created a partial barrier between moist Pacific air masses and the interior portion of the continent. The spread of the Antarctic ice sheet, by tying up atmospheric moisture, also contributed to increased aridity. Woody plants are generally less well adapted to drought than most grass species, and the spread of grasslands consequently occurred at the expense of forests. As the grassland expanded, numbers of grazing and browsing animals increased, an indication that the association of grasses and grazers occurred over a long period of time (Stebbins 1981; Axelrod 1985).

The prairies of Illinois are part of the central grassland, a large triangular-shaped area that has its base along the foothills of the Rocky Mountains from the Canadian provinces of Saskatchewan and Manitoba southward through New Mexico into Texas. The apex of the triangle, the prairie peninsula (Transeau 1935), extends eastward into the Midwest and includes the prairies of Illinois, Iowa, Indiana, Minnesota, Missouri, and Wisconsin with scattered outliers in southern Michigan, Ohio, and Kentucky. Because the Rocky Mountains intercept moist air masses moving westward from the Pacific Coast, the grassland lies in the partial rain shadow to the east. From west to east within the central grasslands, annual precipitation increases from 25–38 cm to 75–100 cm and becomes more reliable; potential evapotranspiration decreases, the number of days with rainfall increases, and periods of low humidity and periodic droughts in July and August decrease (Risser et al. 1981). Associated within this climatic gradient is a shift in the grassland species dominating the vegetation.

Ecologists traditionally have separated the central grassland into three major west–east divisions. The arid western shortgrass prairie is dominated by such species as buffalo grass (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), and hairy grama (*B. hirsuta*) that reach heights of only 30–45 cm. The mixed-grass prairie occupies the middle sector of the central grassland and is dominated by grasses that are 60–120 cm tall, including little bluestem (*Schizachyrium scoparium*), needle-grasses (*Stipa spartea* and *S. comata*), and wheatgrasses (*Agropyron smithii* and *A. dasystachyum*). The prairies of Illinois are in the eastern portion of the remaining division of the central grassland, the tallgrass prairie (Figure 1). In this area of relatively high rainfall, the dominant grasses on mesic sites include big bluestem (*Andropogon gerardi*), Indian grass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*)—grasses that reach heights of 1.8–3.6 m. On poorly drained sites supporting wet prairies, prairie cordgrass (*Spartina pectinata*) and bluejoint grass (*Calamagrostis canadensis*) are dominant species; little bluestem and sideoats grama (*Bouteloua curtipendula*) are important grasses on dry sites (Weaver 1954; Risser et al. 1981; Bazzaz and Parrish 1982). Figure 2 indicates how these major grass species follow a soil moisture gradient.

Illinois prairies, which dominated about 60% of the state prior to the extensive settlement and alteration of the landscape by Europeans, developed since the last glacial advance. According to King (1981), as the last of the Wisconsinan age ice sheet retreated from the northeastern portions of the state, mesic deciduous forests dominated most of the landscape. A drying and warming trend began about 8,700–7,900 YRBP, and prairie began to replace deciduous forests in southern Illinois. Prairie influx into central Illinois occurred

about 8,300 YRBP and concomitantly oak–hickory forest began to replace mesic forest in the northern portion of the state. Prairies occupied much of the state during the Hypsithermal Period (8,000–6,000 YRBP), which was the hottest and driest part of the Holocene. The climate became cooler and more moist following the Hypsithermal, but prairie stabilized throughout much of Illinois (King 1981).

Because of increased rainfall and reduced evapotranspiration, the climate is increasingly favorable for the growth of trees from west to east in the central grassland. Consequently, in Illinois and the rest of the prairie peninsula, the average climate for approximately the past 5,000 years appears to have been more favorable for forest than for grassland. However, this region has had periodic droughts during which the forest retreated and the grasslands advanced or were maintained. To understand factors influencing the persistence of grasslands in this region, we must consider the extremes of climate and not the average. Britton and Messenger (1970) suggested that the droughts that are most detrimental to woody species are those that do not permit deep recharge of soil moisture during the winter months. On soils without drainage restrictions, trees generally root at greater depths than grasses and rely on moisture stored deep in the soil during droughty periods in midsummer. Interestingly, Britton and Messenger (1970) presented data showing that areas of the Midwest that did not experience deep soil moisture recharge during the drought of 1933–1934 approximately corresponded to the prairie peninsula (Figure 3).

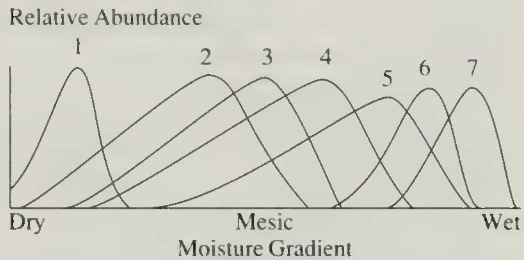

Figure 2. Generalized distribution of major grass species across a soil moisture gradient: (1) sideoats grama, *Bouteloua curtipendula*; (2) little bluestem, *Schizachyrium scoparium*; (3) Indian grass, *Sorghastrum nutans*; (4) big bluestem, *Andropogon geradi*; (5) switchgrass, *Panicum virgatum*; (6) bluejoint grass, *Calamagrostis canadensis*; (7) prairie cordgrass, *Spartina pectinata*. Adapted from Parrish and Bazzaz 1982.

Figure 1. Presettlement distribution of the tallgrass prairie. Adapted from National Geographic (1980) 157(1):43.

Figure 3. Area in which complete recharge of soil moisture did not occur between the summer of 1933 and the summer of 1934 is shown in dark grey; light grey indicates the area of complete recharge. From Britton and Messenger 1970.

Ecologists generally recognize that climate is the most important factor influencing the distribution of vegetation. However, most ecologists believe that prairie vegetation in the eastern United States would have largely disappeared during the past 5,000 years had it not been for the nearly annual burning of the prairies by the North American Indians and the prairie fires set by lightning (Komarek 1968). The role of Indians in maintaining the prairies and the reasons they burned these grasslands have been discussed and documented by various authors (e.g., Stewart 1951, 1956; Curtis 1959; Pyne 1986).

Although many woody species, for example, oaks (*Quercus* spp.), readily resprout after being top-killed by fire, prairie species are generally better adapted to burning than are most woody plants. The adaptation that protects grasses and forbs from fire is their annual growth habit: the plant dies back to its underground organs each year, exposing only dead material above ground (Gleason 1922). Prairie fires become very hot above ground and on the surface of the soil (83 to 680°C) (Wright 1974; Rice and Parenti 1978) but because they move quickly and soil is a good insulator, little heat penetrates the soil. The same adaptation that protects prairie plants from fire also protects them from drought and grazing. Growing points beneath the surface of the soil permit regrowth after intense grazing and protect perennating organs from desiccation during periods of drought or from fire at any time of the year (Gleason 1922; Tainton and Mentis 1984; Anderson 1982,1990).

Grasses generally produce more biomass annually than can be decomposed in a year. This production of excess herbage probably evolved in response to grazing; however, the productivity of grasslands declines when excess plant litter is not removed by fire or grazing (Golley and Golley 1972). Thus, grasslands evolved under conditions of periodic drought, fire, and grazing and are adapted to all three (Owen and Wiegert 1981; McNaughton 1979, 1984; Anderson 1990).

In presettlement Illinois, the vegetation was primarily a shifting mosaic of prairie, forest, and savanna that was largely controlled by the frequency of fire under climatic conditions that were capable of supporting any of these vegetation types. The frequency of fire was largely determined by topography and the occurrence of such natural firebreaks as waterways and dissected landscapes. Fires carry readily across landscapes that are level to gently rolling, but in hilly and dissected landscapes the spread of fire is more limited (Wells 1970; Grimm 1984). Fire tends to carry well uphill because rising convection currents encourage its spread. But as fire moves down slopes, the convection currents tend to retard it by rising upward and working against the downward direction of the moving fire.

The importance of waterways in determining the distribution of forest and prairie in presettlement Illinois was demonstrated by Gleason (1913) through the use of the Government Land Office Records for selected Illinois counties. He found that prairies were more associated with the west sides of streams and bodies of water than with the east sides, and forests were generally found bordering the east sides. Gleason attributed this pattern to prevailing westerly winds that carried fires from west to east; the west sides of waterways, therefore, burned more frequently than the east sides. Forests were most abundant in presettlement Illinois in the northeast Morainal Section (Schwegman 1973) and in the three unglaciated areas of Illinois (driftless area of Jo Daviess and Carroll counties in northwest Illinois, Calhoun County and portions of Pike County in west-central Illinois, and the far southern portion of the state) (Figure 4). In these areas, the dissected nature of the topography and/or the presence of waterways decreased the frequency of fire and encouraged the growth of forests and savannas. Similarly, the Illinoian till plain, which is older and more dissected than the Wisconsinan till plain, supported more forest than the Wisconsinan till plain, especially in the southern portion (Figure 4).

The relationship between topographic relief and vegetational patterns in Illinois has been recently reexamined. Using a map showing the distribution of prairies and timber (forest and savanna) for Illinois, based on the Government Land Office Records (Anderson 1970), and a map of the average slope range for the state (Fehrenbacher et al. 1968), Anderson (1991) determined the simultaneous occurrence of slope categories and vegetation. Most of the prairie vegetation (82.3%) occurred on landscapes with slopes of 2–4%; only 23.0% of the timbered land, usually on floodplains, was associated with this slope category. In contrast,

77% of the timbered land occurred on sites that had slopes greater than 4% (4–7% slope = 35.2% timber and >7% slope = 41.8% timber) (Figure 5). Iverson (1988) also showed that presettlement forests were positively correlated with sloping landscapes.

The relationship between vegetational patterns and topography is illustrated by the presettlement vegetation of McLean County, which is located in the Grand Prairie Division (Schwegman 1973). That relationship is shown in Figure 6 (Rogers and Anderson 1979). Prior to settlement by Europeans, the county was 90% tallgrass prairie, which occupied relatively level landscapes. Savannas and open forests that were dominated by relatively shade-intolerant but moderately fire-resistant oaks (burr, *Quercus macrocarpa*; white, *Q. alba*; and black, *Q. velutina*) occurred on slopes and ridges of glacial moraines. These areas were subject to periodic fires but less frequently than the prairies. Sheltered areas, such as ravines and stream valleys, contained oaks and hickories but also a high component of mesophytic, shade-tolerant, and fire-susceptible tree species—elms (*Ulmus* spp.), ashes (*Fraxinus* spp.), and maples (*Acer* spp.).

Figure 4. Areal distribution of the dominant till formations and unglaciated portions of Illinois. Adapted from Willman and Frye 1970.

The presettlement prairies of Illinois were drastically altered by the influx of European settlers who converted essentially all of the prairie lands to agriculture. The earliest settlers entered the unglaciated southern portion of the state. This was a familiar landscape for these people who were mostly hunters and trappers from forested regions of Tennessee, Kentucky, and West Virginia. As they migrated northward, they followed the fingerlike traces of forest along the major waterways and initially avoided the larger tracts of prairie. For a variety of reasons, the larger tracts of prairie were avoided in favor of smaller tracts of prairie adjacent to waterways and timber. The settlers needed water for their livestock and to turn waterwheels, and timber was needed for fuel and building materials. In addition, the large tracts of prairie exposed the settlers to the force of winter storms. Timber was considered such an important commodity on the prairie that counties were not allowed to form as governmental units until residents could demonstrate that they had access to timber to support development (Prince and Burnham 1908).

Ironically, some of the earliest settlers believed that prairie soils were infertile. They had been familiar with life in the forest and thought that soil incapable of supporting trees would not be productive for crops. Furthermore, turning over the thick prairie sod was an almost insurmountable obstacle to early prairie farmers until John Deere invented the self-scouring steel plow in 1836. Even after settlers had learned of the fertility of the prairie soil and could raise large crops, many of the larger tracts of prairie remained unsettled because the lack of transportation to get crops to distant markets inhibited expansion onto the prairie. With the coming of the railroads in the 1850–1860s, however, prairies were rapidly converted to cropland (Anderson 1970).

As the prairies were converted to an agricultural landscape, fires, which had swept nearly annually across the prairie in presettlement times, were actively stopped by settlers

who viewed them as a threat to economic security. According to Gerhard (1857: 278), "The first efforts to convert prairies into forest land were usually made on the part of the prairie adjoining to the timber. . . . three furrows were ploughed all round the settlements in order to stop the burning of the prairies . . . ; whereupon the timber quickly grows up." The settlers also indirectly stopped the fires by creating plowed fields and roads that acted as firebreaks.

Cessation of these nearly annual prairie conflagrations furthered the demise of the prairies, and many of them were converted to forests or savanna by invading tree species, the distribution of which was no longer restricted by periodic fires. Prairies continued to persist along railroad rights-of-way. Railroads had been in place before the landscape was extensively disturbed and the rights-of-way, which usually extended for 100 feet on either side of the track, were fenced to keep off livestock. In addition, the rights-of-way were managed with fire. Those fires along with many accidental fires prevented the invasion of woody species and exotic weeds. In the last 10 to 20 years, however, many of the remnant prairies along railroads have disappeared because herbicides are used to manage rights-of-way rather than fire. Then too, abandoned rights-of-way, which often contained the only example of native prairie vegetation in areas as large as a county, have frequently been purchased by an adjacent landowner and converted to cropland.

Within Illinois, tallgrass prairie was the dominant grassland community. Variation in topography, drainage patterns, and soil texture resulted in a variety of prairie community

Figure 5. The distribution of native forest–savanna vegetation and prairie (left) compared to average slope categories (right) in Illinois. Native prairie vegetation is shown as black; native forest-savannah vegetation is shown as white. A slope of 2–4% is shown as white, 4–7% as stripes, and >7% as black. From Anderson 1991.

types. Hill prairies occur in scattered locations along the generally forested bluffs of the major river systems, especially the Illinois and Mississippi. These prairies are relatively small, occupying areas from less than a fraction of an acre to as many as 12 or 13 acres. These xeric prairies often occur on west to southwest facing slopes and are dominated by species such as little bluestem and sideoats grama that are dominant components of the arid mixed-grass and shortgrass prairies to the west of Illinois (Evers 1955). Despite the xeric nature of these sites, many presettlement hill prairies have been eliminated or greatly reduced in area as a result of the exclusion of fire and the subsequent encroachment of woody plants (Kilburn and Warren 1963; Anderson 1972; Ebinger 1981; McClain 1983). Many hill prairies have also experienced a decline in quality as a result of grazing by cattle (Evers 1955).

Sand prairies occur on the deep Pleistocene sand deposits along the Illinois River that were laid down by glacial meltwaters during the Woodfordian substage of the Wisconsinan glacial advance (Willman and Frye 1970). These coarse textured sandy soils have little water-holding capacity and favor the growth of plant species adapted to the droughty conditions that characterize this habitat (Gleason 1907; Vestal 1913). Dominant plant species on sand prairies include little bluestem grass, sand lovegrass (*Eragrostis trichodes*), and sand reedgrass (*Calamovilfa longifolia*). The sand prairie community is more resistant to disturbance than the tallgrass prairie. Many agricultural weeds are adapted to mesic sites and are not effective competitors on sand prairie sites. When weeds become established on tallgrass prairie, however, they can prevent recolonization by tallgrass prairie species (Curtis 1959). Until the expanded use of fertilizers and irrigation, sustained agriculture had not been possible on these droughty, low-nutrient sites and as they were abandoned, the native sand prairie flora frequently became reestablished.

Of the 22 million acres of tallgrass prairie that once covered the Illinois landscape, only about 2,300 acres of high-quality prairie remain (White 1978). The prairie community inadvertently provided the incentive for its own demise. In a grassland community, about two-thirds of the plant mass is located beneath the surface of the soil in the form of roots and other underground organs. As these belowground portions of the plant die, they decay in place and greatly enrich the soil with organic matter. The rich and productive soils of most of the Midwest cornbelt, some of the most agriculturally productive soils in the world, had their genesis under prairies. Once the European settlers learned of the fertility of the prairie soil, had the plow that could effectively turn the sod, and could transport their crops to distant markets, the prairies of Illinois disappeared quickly.

Today, however, there is growing interest by the scientific community and the general public in saving and restoring the prairie. The esthetic values of prairie landscapes are being appreciated by a growing number of persons and the potential value of prairie plants in a system of sustainable agriculture is drawing attention from several sources. Efforts are being made to develop one of the native grasses (eastern gama grass, *Tripsacum dactyloides*) into a perennial grain crop (Eisenberg 1989) and to expand the use of warm-season native grasses as a source of forage in combination

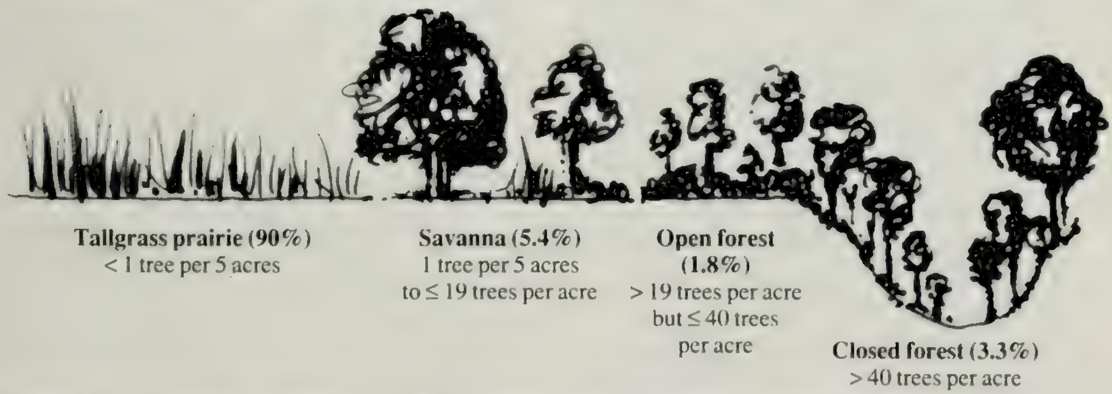

Figure 6. Presettlement vegetation of McClean County, Illinois, in relation to topography about 1820. Adapted from Anderson 1990.

with cool-season domestic grasses. The cool season domestic grasses, such as orchard grass (*Dactylis glommeratus*) and smooth brome (*Bromus inermis*), provide forage during the early and late (cool) portions of the growing season. The warm-season prairie grasses, which maximize growth in July and August, produce a high-quality forage in the middle of the summer when the productivity of the cool-season species is low. As a result, cattle are provided with abundant, good-quality forage throughout the growing season.

It is interesting to note that such cool-season grasses as the exotic Kentucky bluegrass (*Poa pratensis*) were favored over native grass species by the European settlers as forage for livestock. Bluegrass provided forage a month earlier in the spring and a month later in the fall than the native species and was favored for this reason (Prince and Burnham 1908). Because the native grasses had evolved under a system of intermittent grazing pressure, they were eliminated when exposed to continuous grazing. After a couple of years of continuous grazing, native species declined, and the Kentucky bluegrass invaded and dominated.

In Illinois, the tallgrass prairie ecosystem is gone. Yet, the interest in preserving the remaining remnant prairies is strong, including the efforts of such private groups as the Grand Prairie Friends and The Nature Conservancy and such governmental agencies as the Illinois Department of Conservation and the Department of Transportation. Plantings of prairie grasses now diversify the vegetation along many interstate highway rights-of-way. An increasing number of native prairie forbs, the nongrass plants ("flowers") of the prairie, and prairie grasses are being sold by commercial nurseries and seed growers. These forbs include blazing star (*Liatris* spp.), purple cone flowers (*Echinacea pallida* and *E. purpurea*), yellow cone flower (*Ratibida pinnata*), and others. These efforts ensure that future generations of Illinoisans, like the earliest visitors to the state, will have the opportunity to observe prairie life and be inspired by the pleasant colors of tall prairie grasses in the fall and shooting stars (*Dodecatheon media*) and lavender phlox (*Phlox pilosa*) in the spring.

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Prairie and Savanna-restricted Insects of the Chicago Region

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Abstract. Numerous remnants of the presettlement prairies and savannas of the Chicago region have survived. Unfortunately, most are very small and degraded. Nearly all are isolated within vast expanses of human-dominated landscape. For the past nine years, I have surveyed grasshopper, katydid, froghopper, leafhopper, treehopper, butterfly, and macro moth (in part) communities on a variety of these remnants in an attempt to gauge the status and site size requirements of the remnant-restricted members of these groups.

Few of the species considered in this study (probably less than 5%) have been extirpated. Most, perhaps as many as 80–90%, have adapted to our degraded modern landscape and can be found in a variety of human-dominated settings. Among the 10 to 20% that are restricted to native grassland remnants, roughly half are seemingly secure, surviving on at least a dozen protected sites. Approximately one-fifth of the remnant-restricted species are known from fewer than six sites and may be endangered within this area.

Most of the remnant-restricted insects considered in this study have survived on relatively small sites. One-third have been found on sites smaller than 5 hectares. Two-thirds have been found on sites of less than 40 hectares. More than four-fifths have been recorded on two or more sites of less than 300 hectares. (Even sites as small as 1 hectare can support a few restricted species.) Site size is clearly an important determinant of butterfly diversity on smaller remnants (1–60 ha) in this region.

Prairie Birds of Illinois: Population Response to Two Centuries of Habitat Change

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The landscape of Illinois has changed considerably over the last two hundred years. The once extensive, unbroken stretches of prairie have given way to agricultural crops, and this shift has had a substantial impact on the state's bird fauna. The purpose of this paper is twofold: to examine how the prairie bird fauna of Illinois has responded to changes in the state's landscape and to discuss how a highly fragmented landscape may be affecting prairie bird populations.

POPULATION STUDIES 1800–1900

Prior to European settlement, prairie occupied approximately 8.5 million hectares in Illinois, nearly two-thirds of the state (Anderson 1970). The area of prairie was over 1.5 times that of forests, which at approximately 5.5 million hectares was the next most abundant habitat type (Graber and Graber 1963). The composition of the presettlement bird fauna in Illinois is not well known. Current data, however, show that prairies support relatively low densities of breeding birds. Bird densities in tallgrass prairie habitat average roughly 1.8 pairs per hectare (Cody 1985). Comparable densities for eastern deciduous forests are 8.7 pairs per hectare (obtained from 87 breeding bird studies published in *American Birds*, volumes 37 and 38). Because of the low density of birds in prairie habitat, Graber and Graber (1963) estimated that only 35–40% of the presettlement bird fauna of Illinois was composed of prairie birds; forest birds, however, may have accounted for as much as 55–60%.

Unfortunately, by the time much of the early ornithological work was conducted within Illinois (1850–1900), considerable losses of prairie habitat had already occurred. By 1850 prairie habitat had been reduced to 2.1 million hectares (Graber and Graber 1963), a reduction of almost 75% or roughly 3.5% per year since 1810. We can, therefore, reasonably assume that some changes in the prairie bird fauna had occurred prior to any detailed study. Nevertheless, the works of Ridgway (1873, 1889, 1895) for central and southern Illinois and Nelson (1876) for northern Illinois can be used to estimate prairie bird abundances in the state prior to 1900 (Table 1).

A number of prairie bird species initially benefited from the conversion of prairie to farmland. Those that benefited most include the horned lark, vesper sparrow, and greater prairie-chicken. The increase in horned larks and vesper sparrows was largely due to their ability to colonize and breed in cultivated habitats, which by 1900 had become the most abundant habitat type in the state (Graber and Graber 1963). The initial opening of the prairies and forests to agriculture produced an intermixed pattern of food and cover that was beneficial to many species of upland game, including the greater prairie-chicken (Westemeier and Edwards 1987). This shift in habitat coupled perhaps with a reduction in the abundance of predatory animals (due to fur trapping and hunting) allowed the prairie-chicken to reach a peak abundance within Illinois of approximately 10 million birds by 1860 (Westemeier 1986; Westemeier and Edwards 1987). Prairie-chickens started to decline soon after reaching their peak abundance. Nelson (1876) listed them as once excessively abundant but now rather scarce in the Chicago region and as less numerous in all the more settled areas of the state due to egg collection by humans, unrestricted hunting, and loss of habitat.

POPULATION STUDIES 1900–1950

During 1906–1909, a systematic survey of the state's birds was conducted by Alfred Gross and Howard Ray of the Illinois State Laboratory of Natural History (Forbes 1913; Forbes and Gross 1922). These surveys provided the

first quantitative estimates of breeding bird populations within Illinois. A summary of the relative abundances of the most common grassland species encountered by Gross and Ray in ungrazed grass, mixed-hay, and pasture from the north and central regions of Illinois are shown in Table 1. Gross and Ray found bobolinks and meadowlarks (eastern and western) to be the most common bird species, accounting for more than 50% of all birds encountered in these habitats. Of the birds listed as abundant or very common by Ridgway (1889, 1895) and Nelson (1876), the greater prairie-chicken, upland sandpiper, and Henslow's sparrow apparently experienced the greatest declines between the mid-1800s and the censuses of Gross and Ray. All three of these species were uncommon or rare by 1906 (Table 1).

In the first paper addressing changes in the bird fauna of Illinois, Ridgway (1915) discussed changes that had taken place in the half century preceding 1915. He cites three prairie birds—the greater prairie-chicken, upland sandpiper, and dickcissel—as experiencing serious declines during this period. The greater prairie-chicken and upland sandpiper were considered on the verge of elimination within Illinois because of shooting and destruction of nests by dogs and cats. The dickcissel had also dramatically declined during this period for "unknown reasons" (Ridgway 1915). Ridgway first noted the dickcissel's decrease around 1885 and stated that by 1915 this species never reached more than one-fourth and usually less than one-tenth its former numbers. Coincidentally, Fretwell (1986) documented a sevenfold increase in grazing pressure between 1870 and 1884 on the dickcissel's primary wintering grounds in Venezuela, a factor that he believed could significantly affect winter resources and, in turn, dickcissel numbers.

POPULATION STUDIES 1950–1989

In 1956–1958, the census routes of Gross and Ray were repeated by Graber and Graber (1963) of the Illinois Natural History Survey

Table 1. Relative abundance of prairie birds within Illinois 1850–1989.

Species	Prior to 1900[1]	1906–1909[2]		1956–1958[3]		1987–1989[4]		USFWS[5]
		%	Rank	%	Rank	%	Rank	% change
Eastern meadowlark[6]	Abundant	25.5	2	20.0	2	11.8	2	–67.0
Dickcissel	Abundant	13.1	3	8.7	4	7.7	5	–46.7
Grasshopper sparrow	Abundant	5.9	5	5.3	6	8.6	4	–56.0
Bobolink	Abundant	25.8	1	9.7	3	11.4	3	–90.4
Henslow's sparrow	Abundant	<1.0	15	<1.0	14	1.6	12	*
Red-winged blackbird	Very common	9.9	4	36.2	1	26.8	1	–18.8
Greater prairie-chicken	Very common	<1.0	13	0.0	16	0.0	16	*
Upland sandpiper	Very common	2.3	9	<1.0	12	<1.0	13	–16.8
Vesper sparrow	Common	1.3	11	1.4	10	<1.0	15	+12.1
Horned lark	Common	4.9	6	4.8	7	<1.0	14	0.0
Field sparrow	Common	4.0	7	2.9	9	5.6	7	–52.6
Song sparrow	Common	2.6	8	1.0	11	3.3	10	–29.3
Savannah sparrow	Common	2.3	10	5.8	5	3.5	9	–58.9
American goldfinch	Common	1.2	12	3.1	8	4.7	8	–42.8
Common yellowthroat	Common	<1.0	14	<1.0	15	5.8	6	– 8.8
Sedge wren	Common	<1.0	16	<1.0	13	2.8	11	–22.5

[1] Relative abundance prior to 1900 based on the works of Nelson (1876) and Ridgway (1873, 1889, 1895).
[2] Relative abundance 1906–1909 based on the censuses of Gross and Ray from approximately 380 ha of ungrazed grass, mixed-hay, and pasture, located in northern and central Illinois (Forbes 1913; Forbes and Gross 1922).
[3] Relative abundance 1956–1958 based on the censuses of Graber and Graber (1963) from approximately 290 ha of ungrazed grass, mixed-hay, and pasture, located in northern and central Illinois.
[4] Relative abundance from the present study (1987–1989) based on censuses of approximately 400 ha of ungrazed prairie and agricultural grasslands in northeastern and east-central Illinois.
[5] Estimated population change within Illinois between 1967–1989 based on United States Fish and Wildlife Service's breeding bird survey (USFWS, unpublished data).
[6] For 1906–1909 and 1956–1958, relative abundance estimates are for eastern and western meadowlarks combined.
*Present on too few routes for accurate trend analysis.

(Table 1). The Grabers believed that the red-winged blackbird, horned lark, and dickcissel had shown large statewide population increases between 1909 and 1956.

Red-winged blackbird numbers had almost doubled since the earlier censuses of Gross and Ray due to the ability of this species to invade nearly all terrestrial habitats within the state (Graber and Graber 1963). Ridgway (1889) noted that although very common, the nests of red-winged blackbirds were always in or in very close proximity to a swamp or marsh. Gross and Ray, however, found red-winged blackbirds in all the grassland habitats they censused in 1906–1909, although 60% of the state's population of these birds still nested in marshes (Graber and Graber 1963). From 1909 to 1956, red-winged blackbird densities within grassland habitats in Illinois increased nearly tenfold. The species had become far more common in grasslands than in marshes, with individuals inhabiting marshes accounting for less than 3% of the state's population (Graber and Graber 1963).

The statewide increase in horned larks between 1909 and 1956 corresponded to their shift from primarily grassland to cultivated habitats, especially row-cropped fields. This switch from a rapidly declining to a rapidly increasing habitat greatly benefited the horned lark, which Graber and Graber (1963) recognized as the species that had increased most dramatically between 1909 and 1956. The Grabers attributed the dickcissel's statewide increase to an expansion in acreage of agriculturally disturbed grasslands, a type of habitat that this species may prefer over true prairie (Kendeigh 1941; Graber and Graber 1963; Zimmerman 1971). Most species of prairie birds, however, had shown either little or no statewide population change between 1909 and 1956 (Graber and Graber 1963). The bobolink, song sparrow, and savannah sparrow showed slight increases, the upland sandpiper and field sparrow slight decreases, and the vesper sparrow, grasshopper sparrow, and American goldfinch no change.

Between 1987 and 1990, I conducted research on the breeding birds of Illinois grasslands; however, my field methods differed from those used by Gross and Ray and the Grabers and direct comparisons are therefore not possible (see Herkert 1991 and Graber and Graber 1963 for descriptions of methods). Nevertheless, a comparison of relative abundances of these species indicates that the current composition of grassland bird fauna is probably very similar to that of the late 1950s (Table 1). Red-winged blackbirds remain the most common species, outnumbering the next most abundant species, the eastern meadowlark, by more than two to one. In fact, four of the five most abundant species are the same in my censuses and in those of Graber and Graber (Table 1).

An estimate of how prairie bird numbers have changed since the Grabers' census can be obtained from data collected by the United States Fish and Wildlife Service's cooperative breeding bird survey (unpublished data). These data from Illinois for 1967–1989 show that nearly all prairie bird species have experienced population declines during this 23-year interval (Table 1). Some of the formerly most abundant prairie bird species, for example, the bobolink, have shown declines as high as 90% during this period. The causes of these recent population declines are not well understood but probably are a consequence of continued loss of grassland habitat within Illinois.

Although the initial loss of prairie habitat within Illinois was rapid and extensive, the reduction of prairie habitat has continued in recent decades. By 1978, less than 1,000 hectares of high-quality prairie remained in the state (Schwegman 1983). The loss of prairie habitat was originally offset by the creation of secondary grasslands such as hayfields and pastures, habitats which the majority of prairie birds found suitable for breeding (Graber and Graber 1963). In fact, none of the characteristic birds of the eastern tallgrass prairie region are considered endemic to prairie habitat (Risser et al. 1981). Acreage of these secondary grassland habitats, however, has also recently declined. For example, the amount of hay within Illinois was reduced by more than half, from 850,000 to 400,000 hectares, between 1960 and 1989 (Illinois Agricultural Statistics Service 1988, 1989). The amount of pasture within Illinois has also been greatly reduced, with pasture occupying only 607,000 hectares in 1987 (U.S. Department of Commerce Bureau of the Census 1989) compared with 2.5 million hectares in 1906. The continued loss of both native and agricultural grassland habitats in Illinois has contributed to an increasingly fragmented landscape.

HABITAT FRAGMENTATION

The process of habitat fragmentation sets off a series of events that can ultimately have a major effect on breeding bird communities. Changes associated with increased fragmentation include a decrease in the total amount of habitat, a decrease in the average size of habitat patches, increased patch isolation, and an increase in the ratio of edge to interior habitat, all of which may have important consequences for breeding birds (Wiens 1989).

The most important consequence of habitat fragmentation is the loss of large amounts of habitat and the resulting losses of individuals, local populations, and possibly even species. Surprisingly, only three species of prairie birds have been extirpated from Illinois despite the extensive loss of prairie habitat (Table 2). Bowles et al. (1980) originally listed four species as extirpated from Illinois, but the sandhill crane has returned to the state as a breeding species (Kleen 1988). The remaining three species (sharp-tailed grouse, swallow-tailed kite, and whooping crane) were extirpated prior to or very shortly after 1900 (Bowles et al. 1980). Another 13 prairie bird species are now considered to be threatened or endangered within Illinois (Table 2), primarily as a direct result of extensive habitat loss. A number of these endangered and threatened species may be on the verge of extirpation within Illinois. The greater prairie-chicken, for example, once one of our most abundant prairie birds, now has a statewide population of less than 100 individuals (R. Westemeier, pers. comm.).

The reduction of the average patch size that accompanies habitat fragmentation also has serious consequences for breeding birds. Small patches may be too small to meet the minimum territory requirements for a species or may lack essential resources necessary for the establishment of populations (Diamond 1975). The responses of individual species to reductions in patch size are variable, but nearly all bird species exhibit a minimum area threshold below which they never occur (e.g., Lynch and Whigham 1984; Hayden et al. 1985; Robbins et al. 1989). Six prairie bird species were never encountered during my research within Illinois on areas of less than 10 hectares (Table 3), despite the fact that the average territory for four of these species (bobolink, savannah sparrow, grasshopper sparrow, and Henslow's sparrow) is typically less than 2.5 hectares (Wiens 1969). Many prairie bird species avoid small areas, and small grasslands have been shown to support impoverished breeding bird faunas (Samson 1980; Howe et al. 1985; Herkert 1991). The number of breeding bird species in grassland fragments is strongly related to fragment size, with large fragments supporting significantly more species than small fragments (Samson 1980; Herkert 1991). In addition, small habitat patches generally support small numbers of individuals, thus greatly increasing the influence of stochastic events on population demography. As a result, small isolated bird populations have been shown to exhibit relatively high turnover rates (e.g., Diamond 1969; Diamond and May 1977; Morse 1977) and therefore a higher probability of local population extinction.

In Illinois, the natural areas inventory (1975–1978) identified only 253 remnants, totaling 950 hectares, of high-quality prairie

Table 2. Extirpated, endangered, and threatened birds of Illinois prairies (from Bowles et al. 1980).

Endangered	Threatened
American bittern	Loggerhead shrike
Yellow rail	Henslow's sparrow
Black rail	Brewer's blackbird
Bachman's sparrow	
Greater prairie-chicken	Extirpated
Swainson's hawk	Sharp-tailed grouse
Short-eared owl	Whooping crane
Northern harrier	Swallow-tailed kite
Upland sandpiper	
Sandhill crane	

Table 3. Minimum areas of encounter for 17 grassland bird species from 24 grassland fragments located in northeastern and east-central Illinois (1987–1989). Grasslands ranged from 0.5 to 650 hectares.

<10 hectares	10–30 hectares
Field sparrow	Bobolink
American goldfinch	Savannah sparrow
Song sparrow	Grasshopper sparrow
Dickcissel	Henslow's sparrow
Ring-necked pheasant	
Sedge wren	>30 hectares
Common yellowthroat	Upland sandpiper
Red-winged blackbird	Northern harrier
Northern bobwhite	
Eastern meadowlark	
Vesper sparrow	

within the state (Schwegman 1983). The majority of these remnants were small, most less than 20 hectares, and would therefore be expected to support very few, if any, prairie bird species. Grasslands of 100 hectares or more may be necessary to support just five prairie interior species (Herkert 1991).

Increases in patch isolation can also increase the probability of local population extinctions due to decreased immigration rates. Island biogeography theory predicts that immigration rates will be affected by both patch isolation and size, with the lowest immigration rates occurring on patches that are small and well isolated from a colonizing source (MacArthur and Wilson 1967). Whether mainland fragments act as true islands with respect to immigration, however, is open to question because mainland fragments are not surrounded by totally inhospitable habitat as are true islands and therefore might not show immigration rates that are strongly dependent on patch isolation. A number of studies conducted in the eastern deciduous forests of North America have demonstrated that isolation does have a significant effect on species richness within forest fragments (Robbins 1980; Howe 1984; Lynch and Whigham 1984; Askins et al. 1987). Researchers working in forests on other continents, however, have found no evidence supporting isolation as a significant factor affecting species richness within fragments (Kitchener et al. 1982; Howe 1984; Opdam et al. 1985). The effects of isolation on immigration rates in midwestern grasslands have not been studied to date.

Harris (1984) points out that island biogeography theory assumes that islands always have a mainland source pool for immigration; for terrestrial fragments, however, the "mainland" source may be lost as a result of the fragmentation process. In this case, the recolonization of mainland fragments must occur between habitat patches. The integrity of the whole system would then depend on the existence of areas large enough to produce enough surplus individuals to provide dispersers as well as maintain stable populations within a particular preserve.

Another consequence of habitat fragmentation is an increase in the ratio of edge to interior habitat as patch size decreases (Butcher et al. 1981; Temple 1986). This increase may result in the loss of species that require interior habitats and an increase in the abundance of edge species (Whitcomb et al. 1981; Ambuel and Temple 1983; Temple 1986). Small grasslands are usually dominated by such nonprairie species as red-winged blackbirds and common yellowthroats and support few prairie interior bird species (Herkert 1991). Moreover, the increase in the ratio of edge to interior habitat may lead to lower reproductive success for nesting grassland birds. Levels of both nest predation and parasitism have been shown to be higher in edge habitats than in grassland interiors, especially if the edge is a field–woodland or field–shrubland border (Best 1978; Gates and Gysel 1978; Johnson and Temple 1986, 1990; Burger 1988).

Finally, we must remember that loss of prairie and grassland habitat in Illinois, and throughout the Midwest, affects birds primarily during the breeding season. The majority of prairie bird species are migratory and spend only a fraction of any given year on the breeding grounds. Similar alterations of wintering and possibly migratory habitat may also significantly affect these bird species. The degree to which events off of the breeding grounds affect prairie birds are not well known. For such species as the dickcissel, however, events on the wintering grounds and migratory routes may be the most important factors affecting distribution and abundance patterns on the breeding grounds in the Midwest (Fretwell 1986). The fact that processes operating outside the boundaries of Illinois affect bird populations within the state does not excuse us from being concerned about events occurring within Illinois, but rather should alert us to the year-round needs of these species. If conservation efforts to preserve prairie birds are to succeed, management efforts must address not only processes operating on the breeding grounds within Illinois but the migratory and wintering needs of these species as well.

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Session Three: Wetlands

What would the world be, once bereft
Of wet and wildness? Let them be left,
O let them be left, wildness and wet;
Long live the weeds and the wilderness yet.

—Gerard Manley Hopkins

While most Illinois residents may not consider their state to be particularly wet, early settlers had a very different impression. Writing in 1833, the year Chicago was incorporated as a village, Colbee Benton observed that Chicago "stands on the highest part of the prairie, and in the wet part of the season the water is so deep that it is necessary to wade from the town for some miles to gain the dry prairie. Notwithstanding the water standing on the prairie and the low, marshy places, and the dead-looking river, it is considered a healthy place."

The retreat of the glaciers left numerous large and small streams with many associated wet areas. Much of northeastern Illinois had abundant diverse wetlands, and central Illinois was a montage of wet prairies and marshes. Extensive tracts of tupelo–cypress swamps could be found in the far southern part of the state.

Wetlands are diverse and complex places. The most common wetlands in Illinois are marshes and sedge meadows, although ponds, fens, seeps, wet prairies, swamps, and bogs are also present. Marshes form where water is above the soil surface for all or nearly all of the year—along the margins of ponds, lakes, or rivers, in places sheltered from strong currents and waves. Sedge meadows are usually associated with fens. Here the water level is near or just below the surface most of the year, and this habitat often merges into marshes as the water depth increases. The surface of the vegetation hides countless tussocks or humps formed by the tussock sedge, and these vary in height from a few inches to over a foot. The terms *bog* and *fen* are often used inconsistently, even interchangeably, and considerable confusion has been the result. In general, bogs are acidic and poor in minerals, with most of the water coming from rainfall and surface runoff and most of the new peat developing from sphagnum moss. Fens range from acidic to alkaline and are rich in minerals; much of the water comes from groundwater that has percolated through calcareous bedrock or gravel. Peat is produced primarily by sedges and grasses. Seeps are characterized by groundwater that has reached the surface in a diffuse rather than a concentrated flow. Seeps form when groundwater that has percolated down through porous sand or gravel reaches a layer of impermeable material and flows outward, usually at the base of a bluff or ravine. Swamps are areas where the soil is saturated or covered with surface water for most of the growing season; woody vegetation dominates.

What was formerly looked upon as sources of disease and pestilence, "sacred to the ague and fever," are currently viewed in a new light. The importance of wetlands is only now being realized: they store runoff after major rains and slowly release it; they filter silt and pollutants from water; and they are tremendously productive, providing habitat for a diversity of plants and animals.

Illinois originally had an estimated 8 million acres of wetlands. Since Illinois became a state in 1818, more than 95% of these have been drained with a concomitant loss in the natural processes that wetlands provide. High-quality wetlands that reflect presettlement conditions are exceedingly rare today; only about 6,000 acres remain.

The papers presented at this session reviewed the state of our wetlands, documenting what has been lost as well as what must be restored or preserved. Particular attention was given to the plants and animals that depend on the unique habitats of wetlands.

Aquatic and Wetland Plants of Illinois

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Abstract. Over 100 of the 172 families of vascular plants growing without cultivation in Illinois have species adapted to aquatic or moist soil habitats. These wetland plants range from ferns and their allies to conifers to flowering plants. Growth forms include herbs, shrubs, and trees, any of which may function as the dominant species of a plant community or as minor components. Some important wetland plant families in Illinois are the sedge family (Cyperaceae), grass family (Poaceae), pondweed family (Potamogetonaceae), duckweed family (Lemnaceae), smartweed family (Polygonaceae), and sunflower family (Asteraceae). In providing for their own growth and reproduction, these plants make up the vegetation component of wetlands and provide much of the food, nesting cover, and escape cover for wetland animals.

Common aquatic and emergent species of wetland communities in Illinois include coontail (*Ceratophyllum demersum*) beneath the surface of calm waters, duckweeds (*Lemna* sp.) floating on the surface, bulrushes (*Scirpus* sp.) and cattail (*Typha latifolia*) in marshes, buttonbush (*Cephalanthus occidentalis*) in shrub swamps, and bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) in wooded swamps. A wider variety of species occupy moist soil communities as opposed to aquatic communities.

Breeding Biology and Larval Life History of Four Species of *Ambystoma* (Amphibia: Caudata) in East-central Illinois

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Abstract. Temporary aquatic habitats, whether roadside ditches, flooded fields, or woodland ponds are essential in maintaining the biodiversity of Illinois. Nineteen species of Illinois amphibians (50% of the state's species) depend on such habitats for breeding. Two species of reptiles breed in those habitats, and 8 to 10 more use them as foraging areas. In addition, these temporary aquatic habitats are important for many invertebrate species.

Kickapoo State Park, located in Vermilion County, Illinois, provides just such temporary aquatic habitats, and this paper records my observations of the breeding biology and larval history of four species of salamanders, genus *Ambystoma* (Amphibia: Caudata) in that setting from 1973–1984.

Ambystoma opacum migrated to the dry beds of two vernal hilltop ponds at Kickapoo State Park in late September or October. The females oviposited under the mat of leaf litter that covered the pond beds and abandoned the eggs in late fall. *Ambystoma platineum*, *A. texanum*, *A. maculatum*, and *A. platineum* x *A. texanum* hybrids migrated to the ponds under stimulus of rains in February and March, provided groundwater was sufficient to fill the ponds to a depth of at least 25 cm. *Ambystoma maculatum* migrated 3–7 days later than the other spring-breeding species. In years when no standing water was present in the ponds, spring migration was prolonged or involved few animals. *Ambystoma texanum* and *A. maculatum* males deposited beds of spermatophores in different locations on the pond bottoms. The gynogenetic *A. platineum* used sperm from the *A. texanum* spermatophores to initiate cleavage of their eggs, and fertilization occasionally occurred. *Ambystoma platineum* and *A. texanum* laid eggs in water less than 30 centimeters deep; *A. maculatum* laid eggs in water at least as deep as 30 centimeters.

Ambystoma opacum larvae hatched within 24 hours after the ponds filled in the spring. Eggs of the other species hatched in 3–6 weeks. Larvae grew little for 2 weeks and then grew rapidly for about 1.5 months. Little further growth occurred before transformation.

Larvae usually transformed in late May (*A. opacum*) or late June (the other species). *Ambystoma opacum* larvae were always able to transform, but in most years the ponds dried before most, if not all, of the larvae of the other species could transform. Larvae are opportunistic feeders, and their food included volvocids, ostracods, branchiopods, annelids, insects, and in the case of *A. opacum*, the larvae of other salamanders.

Ecological Integrity of Two Southern Illinois Wetlands

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Palustrine and riverine wetlands in Illinois are increasingly rare ecosystems. Unfortunately, the declining wetland habitat in Illinois is not an isolated phenomenon (Mitsch and Gosselink 1986; Illinois Department of Conservation 1988). Wetlands across this country are in jeopardy due to drainage for a variety of human endeavors, primarily agriculture, or to the associated and chronic but less dramatic threat, soil erosion.

The presettlement area of wetlands in this country is difficult to ascertain, and estimates vary from 51 to 87 million hectares (Greeson et al. 1979). The rapidity with which our wetlands disappeared is difficult to comprehend. By the early 1950s, 35% of the wetlands in this country had already been drained. Federal bureaucracies were given unbridled authority to drain any wetland deemed a nuisance. In the eastern United States, the U.S. Army Corps of Engineers and the USDA Soil Conservation Service played major roles in the destruction of wetlands. The Army Corps destroyed large wetlands while the Soil Conservation Service destroyed smaller ones. Drainage tiles were installed throughout wetlands and quit discharging only when no more water was left to drain. Large and small ditches were dug to expedite drainage and are dramatically illustrated on most topographic maps of southern Illinois. Many of the largest ditches were given quaint yet telling names, for example, Post Creek Cutoff, which was dug in the early 1900s and continues to disrupt the natural hydrological dynamics of the wetlands along the Cache River of southern Illinois. Smaller ditches generally remain unnamed, such as the one dug in an as yet incomplete effort to drain Lovets Pond, a remnant of the once vast Mississippi River floodplain wetlands of southern Illinois. That ditch was most likely dug overnight during the fall of 1986. From 1950 to 1970 another 8.5% of the nation's wetlands were lost, approximately 186,000 hectares per year over the twenty-year period and an area almost twice the size of the Shawnee National Forest.

Most (95%) of the wetlands in the United States are inland and those are incredibly diverse, ranging from the upland, subalpine swamp-meadows of Yosemite to the lowland pitcher-plant bogs of southern Alabama. Of all wetland types (see Cowardin et al. 1979), none is more threatened than the emergent wetlands, those characterized by erect, rooted, herbaceous hydrophytes (excluding mosses and lichens), or the forested wetlands, those characterized by woody vegetation at least 6 meters tall. The former is found in Lovets Pond, and the latter along the Cache River. Nationwide these two wetland types disappeared at a rate approaching 10% each year from 1950 to 1970. This rate has diminished but not nearly enough.

Illinois has the regrettable distinction of having lost more of its wetlands than most other states, and only 5% of our original wetlands are left. Obviously, Illinois needs to preserve all of its remaining wetlands. To do so would provide greater assurance that the state's biodiversity would not decrease to exclude even fairly common but uncelebrated species like the crawling water beetles (*Peltodytes* and *Haliplus* spp.). One cannot be optimistic about future preservation efforts because federal and state laws and their implementation are "too little too late" to prevent even state agencies from destroying wetland habitat. To illustrate, the Illinois Department of Conservation is currently entertaining a proposal to destroy an old-growth bottomland forest wetland in Horseshoe Lake Conservation Area in Alexander County. Public opposition to the project may prevail, but current law and regulation would make that destruction legal.

An immediate response is essential. We need to identify and prioritize the Illinois wetlands in greatest jeopardy, a task not easily accomplished. Many practical and theoretical questions must be answered in the process, for

example, "What size do wetlands need to be to assure their integrity and to preserve maximum biodiversity?" Given present understanding and adequate financial resources, the best answer is to preserve the largest areas possible. In Illinois, however, most of the remaining wetlands are small, isolated islands such as Lovets Pond. Small as these are, they cannot be ignored, and we cannot allow ecological theory to be used as an excuse for not preserving or protecting them. If we accept that only large, nearly pristine areas should be placed on a priority list, we assure further decreases in the state's biodiversity because small wetlands do harbor diverse communities, and in many cases those communities appear to be stable. In fact, small wetlands like Lovets Pond may presently have greater ecological integrity than larger, heavily silted ones like those along the Cache River. By ecological integrity I mean the relative disparity between the abundance and diversity of the aquatic fauna in a given system relative to that which could reasonably be expected to occur in the same system if it were undisturbed. A close look at the macroinvertebrate communities of Lovets Pond and the Cache River wetlands (Figure 1) provides evidence for this contention. Acknowledging the value of small wetlands does not of course mean that we should not fight for the greatest protection possible for larger areas such as the Cache wetlands. Although these areas may be seriously compromised, they nevertheless contain pockets of diversity that might serve as epicenters of re-invasion for an entire area if allowed to do so.

Lovets Pond was once part of a wetland system that covered a large area of the Mississippi River bottoms of southern Illinois

Figure 1. Location of Lovets Pond and the Cache River, the two Southern Illinois sites in this study.

(Jackson County and others). Now, this once vast ecosystem is reduced to a 16-ha remnant that is surrounded by a lowland forest that increases its size to 65 ha. This island is totally enclosed by intensive agriculture. When I began to investigate the ecological integrity of Lovets Pond, I shared the bias of many biologists who are convinced that preserving small areas does not protect enough biodiversity to justify the cost. This contention may be true for large organisms but what about small ones? In long- and short-term scenarios, many species not in need of large areas may perhaps be protected within small, isolated systems.

The Cache River wetlands were also once part of a much larger system (114,000 ha). Only 1% of this vast wetland complex remains, with Heron Pond, a beautiful state nature preserve, the best-known area. At the present time, about 14,000 ha are being considered for inclusion in the proposed Cypress Creek National Wildlife Refuge. The area is an important wintering ground for migrating waterfowl and contains other unique features, including several bald cypress trees over 1,000 years old that represent the oldest living organisms east of the Mississippi River. Agricultural activity occurs throughout the area and forms the borders of most of the remaining wetlands.

SITE DESCRIPTIONS AND METHODS

Lovets Pond. The investigation of the macroinvertebrate communities of Lovets Pond during 1986 focused on two questions (Phillippi and Peterson 1986). Are the communities diverse and distinct from one another? And if so, are the communities distributed to correspond to the vascular plant communities? Because vascular plants are the major substrate for the attachment of nonbenthic macroinvertebrates, distinctiveness among the macroinvertebrate communities might well be realized along a gradient similar to that observed for the vascular plants.

In order to answer these questions, one site was selected for investigation in each of the four major plant communities: open pond, shrub swamp, true swamp, and marsh (Figures 2–5). During 1986, these communities were connected by water for varying amounts of time. The open pond and the shrub swamp were connected the longest, and the true swamp was

connected to the previous two for a shorter period. The marsh was isolated from the other three for most of the year. The open pond community is edged with buttonbush (*Cephalanthus occidentalis*), and by early summer the surface is almost totally covered with yellow pond lily (*Nuphar luteum*). Water in the open pond community was about 1–2 m deep. The shrub swamp community surrounds the open pond and is dominated by an impenetrable thicket of buttonbush with a few black willows (*Salix nigra*) scattered throughout. Thick stands of lizard's-tail (*Saururus cernuus*) occur along its edge. In general, 20–30 cm of water covered this community during the winter and spring. The true swamp is fully forested with a variety of tree species, including pumpkin ash (*Fraxinus profunda*), red maple (*Acer rubrum*), and water locust (*Gleditsia aquatica*). Water covered the forest floor (10–12 cm) only during the winter. The marsh, dominated by graminoid plants, is the smallest (1 ha) and most isolated of the four communities. It is maintained by periodic fires set by farmers to prevent the lowland forest from encroaching onto their fields. The amount of silt covering the bottom of each of the four communities was minimal.

Two unit-effort dipnet samples of the macroinvertebrate community were taken from each plant community on six dates at four- to

Figure 2. Open pond community of Lovets Pond in mid-April 1986. The thick growth of yellow pond lily (*Nuphar luteum*) obscures the coontail (*Ceratophyllum demersum*) and pondweed (*Potamogeton* spp.) that are scattered throughout. Photo by author.

Figure 3. Shrub swamp community of Lovets Pond in mid-June 1986. The almost impenetrable growth of buttonbush (*Cephalanthus occidentalis*) in the background is surrounded primarily by lizard's tail (*Saururus cernuus*). Photo by author.

Figure 4. True swamp community of Lovets Pond in mid-June 1986. New growth of arrow arum (*Peltandra virginica*), foreground, covers the lowest points in this community. A variety of tree species are seen in the background, including pumpkin ash (*Fraxinus profunda*), water locust (*Gleditsia aquatica*), and red maple (*Acer rubrum*). Photo by author.

Figure 5. Marsh community of Lovets Pond in mid-May 1986. Such graminoid plants as bur reed (*Sparganium eurycarpum*), giant bulrush (*Scirpus tabernaemontanii*), and common cattail (*Typha latifolia*) surround the marsh edge. Duckweeds (*Spirodela* spp. and *Lemna* spp.), water meal (*Wolffia* sp.), and sponge plant (*Limnobium spongia*) cover the surface by summer. Photo by author.

six-week intervals, January through June 1986. Samples were preserved and later sorted and identified to the lowest practical taxon.

Cache River and Wetlands. During the summer of 1986 a team of biologists (Phillippi et al. 1986) surveyed the aquatic fauna at 23 sites within the Cache River drainage (Figure 6). Two dipnet samples were taken from a representative portion of each of the sites and the organisms sorted and identified to the lowest practical taxon.

Figure 6. Large bald cypress (*Taxodium distichum*) along the Cache River and its wetlands provide a major attraction for canoeists. Photo by Marti Crothers.

RESULTS AND DISCUSSION

Lovets Pond. The true swamp and marsh communities of Lovets Pond contained the highest number of macroinvertebrate taxa: the lowest number was found in the open pond (Table 1). Samples taken from the true swamp and shrub swamp communities yielded the largest number of individuals; once again, the open pond yielded the lowest number (Table 1).

The number of taxa and individuals in each community fluctuated in a roughly similar fashion across the seasons; however, no pattern within or across the four communities in regard to the diversity (H') of macroinvertebrates was discernible (Figure 7). No single plant community always harbored the highest or lowest species diversity. Even so, the four plant communities contained distinct macroinvertebrate assemblages, at least qualitatively, and this distinction was demonstrated using Jaccard's similarity coefficients and group average clustering (Figure 8). Cluster 1 is predominated by the shrub swamp macroinvertebrate community, cluster 2 by the true swamp, and cluster 4 by the open pond community. The macroinvertebrate community inhabiting the marsh is indistinct from those of the other three communities even though the marsh is the most isolated of the four communities. These data suggest that this small wetland harbors distinct and diverse macroinvertebrate communities—communities that are known to be dramatically affected by human-caused changes in substrate and water quality (Greeson et al. 1979). From the practical viewpoint of conservation biology, the ecological integrity of Lovets Pond can be considered good and thus worthy of protection.

Cache River and Wetlands. Approximately 230 aquatic and semiaquatic macroinvertebrate taxa were collected from the 23 sites. The number of taxa and individuals at

Table 1. Total number of taxa and individuals for the four major plant communities of Lovets Pond. Ranges are given in parentheses.

	Open pond	Shrub swamp	True swamp	Marsh
Total number of taxa	37	52	58	59
(Number per sample)	(8–20)	(14–30)	(10–30)	(11–26)
Total number of individuals	1,042	4,034	4,807	2,200
(Number per sample)	(113–241)	(526–982)	(257–1,259)	(113–769)

each site ranged from 21–66 and 212–2,735, respectively. Only 7% (17 taxa) were found at 10 or more sites. Of those 17 taxa, 6 were crustaceans (aquatic sowbugs, sideswimmers, shrimps, and crayfishes) and 6 were surface or water-column dwelling beetles (Coleoptera) or bugs (Heteroptera). Over 20,500 individuals were examined, excluding those taken from qualitative samples. The clubtail dragonfly (*Ariogomphus maxwelli*) was observed and/or collected at 4 of 23 sites. This species was known from only a few Gulf Coast states until June of 1985 when a single adult male was collected at Mermet Lake in Massac County, Illinois. Thus, the Cache population may be the only viable one in the state. Sampling also yielded such rare to uncommon bugs as the water scorpion (*Nepa apiculata*) and such common but hard to collect bugs as the marsh treader or water measurer (*Hydrometra martini*). In the sites most disturbed with a heavy silt load, at least a few surface-dwelling insects (for example, *Gerris marginatus* and *Trepobates* spp.) were found. *Gerris marginatus* is perhaps the most common strider in the Cache system.

To assess the ecological integrity of the various Cache sites, species diversity measurements (H') were calculated and can be compared with those found at Lovets Pond. Four sites have a relatively high species diversity (0.898–1.131): the Cache River at Highway 37, Snake Hole, Eagle Pond, and Long Reach. The Cache River at Highway 37 is a highly disturbed site. The north bank has been cleared and a levee built. The channel has been dredged and carries a very heavy silt load. Long Reach is also a heavily silted portion of the main channel. Snake Hole is a well-shaded pond located at the base of a rocky-boulder cliff in an area known as Little Black Slough. This state-owned site is generally the least silted of any of the Cache wetlands. Eagle Pond, also heavily silted, is a popular canoeing destination because of its picturesque cypress knees and buttonbush thickets. Sites with moderate macroinvertebrate species diversity (0.651–0.834) are heavily silted, including Wildcat Bluff/Watson Pond and Short Reach, both owned by the Illinois Department of Conservation. The other 5 sites with moderate diversity are privately owned. The remaining 12 sites have low species diversities

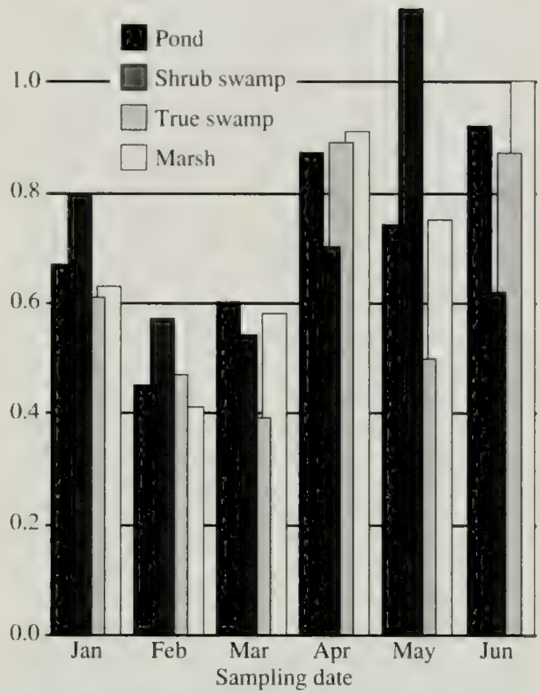

Figure 7. Shannon diversity (H') values (N=2) for the macroinvertebrate communities inhabiting the four major plant communities of Lovets Pond.

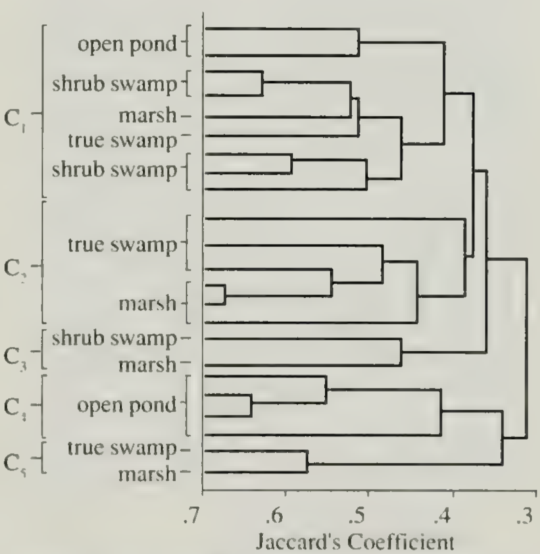

Figure 8. A clustering of the macroinvertebrate communities inhabiting the four major plant communities of Lovets Pond using group average clustering of the Jaccard's coefficients of similarity.

(0.170–0.612), including Limekiln Spring and Slough which is owned by The Nature Conservancy and is generally considered "protected." That site exemplifies the major threat to all the remaining Cache wetlands—excessive habitat destruction due to siltation from agricultural endeavors. Even the integrity of the areas "protected" by the state, by The Conservancy, or by other private groups is being threatened by siltation, which is obliterating most of the available aquatic habitat. The quality of the adjacent terrestrial habitat is variable; some sites are cleared of all vegetation and others have mature, high-quality forests or swamps. Sites with the most disturbed terrestrial component generally have the least diverse aquatic component. Even though the data reveal that macroinvertebrate species diversity is generally low, enough islands of diversity seem to exist to reclaim the area if it were protected from further siltation and other degrading influences. The ecological integrity of the Cache and its wetlands cannot, however, be considered good, especially in light of the excessively silted substrate of the areas I visited.

CONCLUSIONS

I have examined the ecological integrity of two southern Illinois wetlands: one small, Lovets Pond, and a much larger one, the Cache. I have concluded that if drastic measures are not immediately initiated (such as the proposed Cypress Creek National Wildlife Refuge), the future of the Cache River system is bleak, primarily due to excessive siltation. On the other hand, Lovets Pond appears adequately protected from siltation by a forest buffer.

We should act now to preserve both systems and all other Illinois wetlands, regardless of size. Large, disturbed systems such as the Cache may recover, thereby preserving a large portion of the biodiversity of Illinois. Small systems such as Lovets Pond also serve to preserve their share of biodiversity.

ACKNOWLEDGMENTS

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Status and Distribution of Wetland Mammals in Illinois

Joyce E. Hofmann, Illinois Natural History Survey

Wetlands are highly productive and diverse habitats that supply important resources for many mammalian species (Fritzell 1988). The objectives of this paper are to list the mammals that are found in the wetlands of Illinois, to identify species that are threatened or endangered, and to discuss the distribution of wetland mammals within the state, especially those restricted to wetland habitats. Only palustrine wetlands, rather than riverine or lacustrine systems, are considered. These shallow water habitats are categorized as palustrine emergent (sedge meadow, marsh, bog, and fen), palustrine scrub-shrub, and palustrine forested (swamp and seasonally or temporarily flooded forested wetland) wetlands (Cowardin et al. 1979). Illinois mammals that inhabit these types of wetlands are listed in Table 1.

Most of the mammals in Table 1 are terrestrial or semiaquatic. Bats are not typically considered wetland mammals, although any Illinois species might well forage above marshes or bogs or along the edges of swamps. Research conducted by the Illinois Natural History Survey and the Illinois Department of Conservation revealed that forested wetlands in southern Illinois provide roosting sites for three species of bats. In May 1988, a radio-tagged pregnant Indiana bat was found roosting behind loose bark on a dead American elm (*Ulmus americana*) in a wetland created by subsidence in Saline County. A lactating southeastern bat was radio-tracked to the hollow base of a living tupelo gum (*Nyssa aquatica*) in Little Black Slough in Johnson County during the summer of 1989; she shared this roost with at least 100 other individuals. Four Rafinesque's big-eared bats were also found roosting in a tupelo gum in the slough during that summer. To stress the importance of palustrine forested wetlands to these three endangered species, I have listed them in Table 1. Other species of bats also roost in trees during the summer, although little is known about their specific habitat preferences (Barbour and Davis 1969; Hoffmeister 1989). Species likely to roost in forested wetlands include the silver-haired bat (*Lasionycteris noctivagans*), northern long-eared bat (*Myotis septentrionalis*), and evening bat (*Nycticeius humeralis*).

Table 1 includes one federally endangered species, the Indiana bat (Endangered Species Act, 16th U.S. Congress, docket 1531); three state endangered species, the southeastern bat, Rafinesque's big-eared bat, and river otter; and three state threatened species, the marsh rice rat, golden mouse, and bobcat (Illinois Administrative Code, Title 17, Chapter I, subchapter c, part 1010.30, as amended March 17, 1989). These seven species and the swamp rabbit (Kjolhaug et al. 1987) are uncommon in Illinois; all other species in Table 1 range from relatively common to abundant (Hoffmeister 1989). The beaver and white-tailed deer are now common even though both species had been nearly extirpated from the state by the end of the 19th century (Pietsch 1954; Pietsch 1956; Hoffmeister 1989).

Some of the species in Table 1 have restricted ranges within Illinois. The southern short-tailed shrew, big-eared bat, southeastern bat, swamp rabbit, marsh rice rat, and golden mouse occur only in the southern portion of the state (Ellis et al. 1978; Feldhamer and Paine 1987; Kjolhaug et al. 1987; Hoffmeister 1989; Illinois Natural Heritage Database). The main breeding population of river otters is along the Mississippi River north of Rock Island (Jo Daviess, Carroll, Whiteside, and Rock Island counties); a smaller population may occur in the Heron Pond–Little Black Slough area of the Cache River drainage (Johnson County) in southern Illinois (Anderson 1982). Most bobcats probably occur in the northwestern and southernmost portions of Illinois where relatively large expanses of suitable habitat remain (Illinois Natural Heritage Database). The Virginia opossum, southern flying squirrel,

beaver, white-footed mouse, woodland vole, muskrat, house mouse, meadow jumping mouse, gray fox, raccoon, mink, and white-tailed deer, on the other hand, occur throughout the state (Hoffmeister 1989). The remaining species in Table 1 have ranges that cover much of Illinois. The meadow vole and least weasel occur in the northern half of the state, and the northern short-tailed shrew is found primarily in the northern two-thirds (Hoffmeister 1989). The southeastern shrew and southern bog lemming occur in the southern two-thirds of Illinois, although bog lemmings have been caught in Carroll County (Hoffmeister 1989). The Indiana bat, though rare, has been found in 20 counties in central and southern Illinois during the summer (Illinois Natural Heritage Database). The masked shrew may have a discontinuous distribution in Illinois, occurring primarily in the northern third of the state but also in at least two southern counties (Hoffmeister 1989).

Many species of mammals are habitat generalists. The home ranges of larger mammals, such as the bobcat and white-tailed deer, typically consist of a mosaic of forested areas interspersed with open areas that could include wetlands (Schwartz and Schwartz 1981). Many smaller mammals may be found in a variety of habitats. The masked shrew, for example, is

Table 1. Wetland mammals of Illinois. Terrestrial and semiaquatic species are included if their activities (e.g., foraging, nesting) are conducted entirely or partly within palustrine wetlands; bats are included if they are known to roost in wetlands.

Common name	Scientific name	Habitat[1]
Virginia opossum	*Didelphis virginiana*	FW
Masked shrew	*Sorex cinereus*	M SM B FW
Southeastern shrew	*Sorex longirostris*	M SW FW
Northern short-tailed shrew	*Blarina brevicauda*	M SM B
Southern short-tailed shrew	*Blarina carolinensis*	M
Indiana bat	*Myotis sodalis*	SW FW
Southeastern bat	*Myotis austroriparius*	SW
Rafinesque's big-eared bat	*Plecotus rafinesquii*	SW
Swamp rabbit	*Sylvilagus aquaticus*	SS SW FW
Southern flying squirrel	*Glaucomys volans*	FW
Beaver	*Castor canadensis*	M SW FW
Marsh rice rat	*Oryzomys palustris*	M SS SW
White-footed mouse	*Peromyscus leucopus*	M SM SS FW
Golden mouse	*Ochrotomys nuttalli*	SS SW FW
Meadow vole	*Microtus pennsylvanicus*	M SM
Woodland vole	*Microtus pinetorum*	M FW
Muskrat	*Ondatra zibethicus*	M SW
Southern bog lemming	*Synaptomys cooperi*	M
House mouse	*Mus musculus*	M FW
Meadow jumping mouse	*Zapus hudsonius*	M SM
Gray fox	*Urocyon cinereoargenteus*	FW
Raccoon	*Procyon lotor*	M SS SW FW
Least weasel	*Mustela nivalis*	M
Mink	*Mustela vison*	M FW
River otter	*Lutra canadensis*	SW FW
Bobcat	*Felis rufus*	SS SW FW
White-tailed deer	*Odocoileus virginianus*	M SS SW FW

[1] Palustrine wetland habitats used by these species are coded as follows:
M = marsh
SM = sedge meadow
B = bog
SS = scrub-shrub wetland
SW = swamp
FW = seasonally or temporarily flooded forested wetland
Sources on habitat use: Barbour and Davis 1974; Schwartz and Schwartz 1981; Mumford and Whitaker 1982, Jones and Birney 1988; and Hoffmeister 1989.

abundant in sedge meadows and marshes in northern Illinois but also inhabits sand prairies, flatwoods, fencerows, pastures, and successional fields (Mumford and Whitaker 1982; Mahan and Heidorn 1984; Szafoni 1989). The white-footed mouse has been trapped in sedge meadows and marshes (Mahan and Heidorn 1984; Szafoni 1989) but is more typically an inhabitant of upland forests and shrublands. In fact, few species of mammals are specifically adapted for living in wetland environments (Fritzell 1988). Most of the species listed in Table 1 are not restricted to wetlands and, therefore, their distribution and abundance are not indicative of or significantly limited by the status of wetlands in Illinois. The swamp rabbit and marsh rice rat are the Illinois mammals that are most limited to palustrine wetlands. The beaver, muskrat, and river otter are also closely associated with wetlands but are more aquatic in their habits and could be considered species of rivers, streams, lakes, or ponds. The swamp rabbit and rice rat are uncommon and have limited distributions within the state; the remainder of this paper will discuss their distribution and status in more detail.

The swamp rabbit is a representative of the Eastern-Austral faunal element, the group of mammalian species whose distributions are centered in the southeastern United States (Jones and Birney 1988). Its northern limit is in Illinois and Indiana and coincides with that of the southern swamp forest community at approximately the 24°C temperature isoline (Chapman and Feldhamer 1981). Swamp rabbits rarely occur far from water and inhabit floodplain forests, cypress swamps, and canebrakes (Cory 1912; Layne 1958; Barbour and Davis 1974; Sealander 1979; Chapman and Feldhamer 1981; Hoffmeister 1989). In Indiana, swamp rabbits were found in areas where low ridges were interspersed with small wooded sloughs and grassy marshes (Terrel 1972).

In the early 1900s, the swamp rabbit was known to occur in swamps along the Mississippi and Ohio rivers in Illinois; its northern limits were thought to be a few miles south of Grand Tower in Jackson County and 5 miles below Golconda in Pope County (Howell 1910). The earliest specimens were collected in Alexander and Johnson counties (Cory 1912) and Williamson County (Necker and Hatfield 1941). Cockrum (1949) believed that the swamp rabbit had extended its range during the early twentieth century as far north as Jefferson County. He reported that hunters had killed swamp rabbits in Franklin County during 1935–1936 and in Jefferson County during 1936. More recently, specimens and possible sightings have been recorded in several other counties: Marion, Massac, Perry, Randolph, and Union (Layne 1958); Bond, Calhoun, Gallatin, Lawrence, Wabash, Washington, and Wayne (Klimstra and Roseberry 1969); and Edwards and White (Terrel 1969). These findings indicate a range extending northward to Calhoun, Bond, and Lawrence counties (Figure 1). Whether these new records represent a range expansion or improved reporting is, however, uncertain.

Kjolhaug et al. (1987) of the Cooperative Wildlife Research Laboratory conducted intensive searches for swamp rabbits or their sign (pellets on logs, vegetation clippings, tracks) in 11 southern Illinois counties and limited searches in three others during 1984–1985. Sign was recorded at 22 sites along the Bay Creek and Big Muddy, Cache, Mississippi, and Ohio River drainages in Alexander, Franklin, Jackson, Johnson, Massac, Pope, Pulaski, and Union counties (Figure 1). No sign was found in Gallatin, Lawrence, Saline, Wabash, Wayne, and Williamson counties, although all but Saline had earlier records. Other counties for which previous records exist were not searched during the study by Kjolhaug et al. (1987).

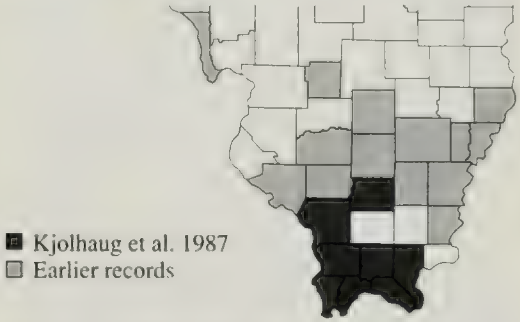

Figure 1. Southern Illinois counties in which swamp rabbit sign was found by Kjolhaug et al. (1987) and earlier records for this species (Howell 1910; Cory 1912; Necker and Hatfield 1941; Cockrum 1949; Layne 1958; Klimstra and Roseberry 1969; Terrel 1969).

The results of the study by Kjolhaug and his colleagues suggest that Alexander, Johnson, Massac, Pulaski, and Union counties support several secure populations of swamp rabbits, whereas this species is present at low densities and with limited distributions in Franklin, Jackson, and Pope counties. Only 12,585 ha in southern Illinois were found to support swamp rabbits, although approximately 2,000 additional hectares of suitable habitat were identified. The state of Illinois was the most important owner of swamp rabbit habitat. The potential habitat for this species in Illinois and neighboring states has been drastically reduced by the construction of levees and drainage ditches and the conversion of bottomlands to agricultural use (Terrel 1972; Barbour and Davis 1974; Korte and Fredrickson 1977; Whitaker and Arbell 1986; Kjolhaug et al. 1987; Hoffmeister 1989). In Indiana, for example, swamp rabbits are now restricted to a single county (Whitaker and Arbell 1986). Fragmentation of bottomland forest and swamp has created islands surrounded by unsuitable habitat, a condition limiting successful dispersal and reestablishment of extirpated local populations. Kjolhaug et al. (1987) concluded that swamp rabbits were unlikely to colonize vacant areas of habitat and that existing populations will continue to be extirpated.

The marsh rice rat (Figure 2) is the only member of this predominantly Neotropical genus with an extensive range in the United States (Honacki et al. 1982). The southern portion of Illinois is at the northern limit of its range, although rice rats once occurred as far north in the state as Peoria County, where their remains have been found at an archeological site (Baker 1936). Rice rats are common throughout much of their range, where they inhabit coastal and freshwater marshes and swamps and areas along lakes, rivers, and streams (Wolfe 1982).

The first modern specimens from Illinois were collected at Olive Branch and Cache in Alexander County (Cory 1912; Necker and Hatfield 1941). McLaughlin and Robertson (1951) collected two specimens in Johnson County and concluded that rice rats were limited to swampy areas within the Coastal Plain Division of the state (Schwegman 1973). More recently, rice rats have also been reported from Franklin, Jackson, Massac, Pulaski, Union, and Williamson counties (Klimstra and Scott 1956; Klimstra 1969; Klimstra and Roseberry 1969; Rose and Seegert 1982; Urbanek and Klimstra 1986; Illinois Natural Heritage Database). In addition, the remains of a rice rat were found in the stomach of a mink collected from an unspecified location in Washington County (Casson 1984). The recent range of the rice rat, inferred from these limited records, extends through the Ozark, Mississippi River Bottomlands, and Shawnee Hills divisions into the Mt. Vernon Hill Country Section of the Southern Till Plain Division.

During 1986–1987 staff members of the Illinois Natural History Survey live-trapped in 17 southern Illinois counties to assess the current distribution of the rice rat (Figure 3; Hofmann et al. 1991). A total trapping effort of 3,517 trap-nights resulted in 1,111 captures of small mammals representing 13 species. Rice rats were captured at 13 sites in 10 counties (Figure 3). They were found for the first time in Hamilton, Pope, Saline, and White counties and were also trapped at new localities in Alexander, Franklin, Jackson, Johnson, Massac, and Williamson counties. Rice rats were not caught in Pulaski, Union, and Washington counties, although earlier records existed. Despite recent trapping efforts, no rice rats have been captured in Gallatin, Hardin, Perry, and Randolph counties. These results suggest that rice rats occur farther to the northeast in the state than indicated by previous records (into the Wabash Border Division). Rice rats may have expanded their range within the state, perhaps using waterways and wet areas along highway and railroad rights-of-way as dispersal corridors; more likely, they were present in Hamilton,

Figure 2. A rice rat live-trapped in Franklin County during the distribution study of 1986–1987. Photo by Marilyn Morris.

Pope, Saline, and White counties but unreported due to limited sampling. Although some potentially suitable habitat for rice rats occurs in Perry, Randolph, and Washington counties, their primary range appears to extend only as far north as Franklin and Jackson counties in southwestern Illinois. In addition to the 10 counties in which rice rats were captured during the Survey's study, they may also occur in Pulaski and Union counties. Existing records, however, do not suggest that they would be common in either county. The only specimen known from Pulaski County was found dead in a field in January 1987 (Illinois Natural Heritage Database), and no rice rats have been reported from Union County since 1958 (Klimstra and Roseberry 1969; Illinois Natural Heritage Database).

During the Survey's study, 132 rice rats were captured, a number that includes at least 99 individuals. Nearly half (45–49 individuals) were trapped at the Saline County site and more than 70% (72–76 individuals) were caught at just four sites in Alexander, Jackson, Pope, and Saline counties. At the nine remaining sites, the number of individuals trapped was

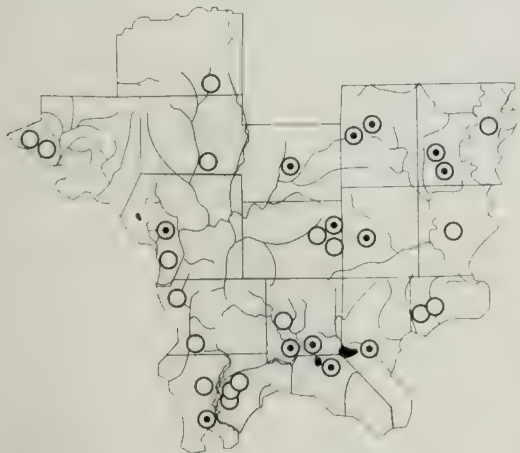

Figure 3. Trapping sites in southern Illinois, 1986–1987 are shown as circles; sites at which captures of rice rats occurred contain dots (Hofmann et al. 1990). The range of this species based on earlier records is indicated in gray (Cory 1912; Necker and Hatfield 1941; McLaughlin and Robertson 1951; Klimstra and Scott 1956; Klimstra 1969; Klimstra and Roseberry 1969; Rose and Seegert 1982; Casson 1984; Urbanek and Klimstra 1986; Illinois Natural Heritage Database).

5 or fewer. Despite the fact that their range within the state is more extensive than had been thought, rice rats do not appear to be common in Illinois and their continued status as a threatened species appears to be warranted.

Areas where rice rats were captured were characterized by standing water and a dense cover of emergent herbaceous vegetation, specifically sedges (*Carex* spp.), rushes (*Juncus* spp.), bulrushes (*Scirpus* spp.), spike rushes (*Eleocharis* spp.), or cattails (*Typha* spp.). Trapping was most successful in roadside ditches along county or state highways and along the shores of ponds and lakes. Since many extensive wetlands in southern Illinois no longer exist, rice rats occupy islands of original or manmade wetland habitat that are often small and widely scattered. Such areas cannot support large populations, and small populations are especially vulnerable to extirpation due to environmental changes, disease, or predation. As with the swamp rabbit, recolonization of a site could be hampered by the large expanses of unsuitable habitat separating it from other populations.

The remaining wetland habitat of the swamp rabbit and marsh rice rat needs to be protected. Such protection should be the highest priority, but habitat enhancement and recreation may also warrant consideration. State and federally owned forested bottomlands could be managed to increase their quality as swamp rabbit habitat (Kjolhaug et al. 1987). Modern surface-mining reclamation techniques have the potential to create habitat suitable for rice rats (Ohlsson et al. 1982; Klimstra and Nawrot 1985). There is no guarantee, however, that such areas would be colonized because existing populations are widely dispersed. Relocation of animals to newly created or existing wetlands may be a useful management procedure. Whitaker and Arbell (1986) recommended reintroduction of swamp rabbits into areas with suitable habitat in Indiana, and the feasibility of relocating rice rats is currently being studied by the Illinois Natural History Survey in southern Illinois. Finally, the fact that most other mammals that use wetlands are flexible in their habitat choices does not mean that there is reason for complacency about the loss of remaining Illinois wetlands.

ACKNOWLEDGMENTS

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Session Four: Streams and Caves

Who hears the fishes when they cry?—Henry David Thoreau

More than half of the 13,200 miles of streams in Illinois have been dredged, channelized, dammed, or altered in other ways. Our rivers and streams suffer from pollution, siltation, and the introduction of exotic organisms. The Illinois River, described by Thomas Jefferson as "a fine river, clear, gentle, and without rapids," has served as Chicago's sewer, a waterway for untold numbers of barges made navigable only by numerous dams, and a repository for much of the eroded topsoil from central Illinois farmland. The "typical" stream in east-central Illinois is a narrow ditch lined with mowed grass, weeds, or row crops, stretching across the landscape and disappearing into the distance. The Cache River in southern Illinois was diverted in 1916 via the Post Creek Cutoff. Designed to alleviate flooding, it cut the river in two, allowing a portion to drain directly into the Ohio River. As a result, the Lower Cache has become a sluggish trickle that even flows backwards upon occasion.

Surprisingly, a few high-quality streams remain in Illinois. The Biological Stream Characterization, an index of stream quality completed in 1989, identified 24 stream segments of excellent quality throughout the state. These total somewhat less than 500 miles, about 4% of the stream mileage in Illinois. Included in this group are segments of the Kishwaukee in northern Illinois, the Vermilion in east-central Illinois, and Lusk and Big creeks in the Shawnee National Forest.

Caves in Illinois have fared somewhat better. Four areas where caves are typically found correspond to major outcroppings of calcareous rocks. More than 480 caves were identified during the 1988 inventory conducted by the Illinois State Museum.

The remarkably stable, insulated environments of caves support a unique biota. For the most part, these organisms are adapted to little or no light and limited food resources. Caves are regarded as natural zoological laboratories where, because of the relative simplicity of the ecosystem, important biological and evolutionary questions can be studied.

One presentation at this session surveyed the nature of Illinois streams—what we have, what we have lost, and what can yet be done by way of restoration and preservation. Two speakers focused on inhabitants of that stream system, the surprisingly diverse and dynamic Illinois fish fauna and the varied mussel populations. The fourth paper described the cave environment and ecosystem, noting the often overlooked values of this unique natural resource.

The Fishes of Illinois: An Overview of a Dynamic Fauna

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Just over ten years ago, Smith (1979) published the most recent comprehensive summary of the Illinois fish fauna. His review revealed 199 fish species, 186 of which were considered native to the state. A major finding was that the Illinois fish fauna is dynamic and that the distributions of many species have changed considerably since the first comprehensive survey of Illinois fishes by Forbes and Richardson ([1908], 1920). Because of introductions of alien species, discoveries of species new to Illinois, and rediscoveries of species formerly thought to be extirpated, the composition of the Illinois fish fauna is in need of clarification.

In the past decade, the greater redhorse, *Moxostoma valenciennesi* (Seegert 1986), and the cypress minnow, *Hybognathus hayi* (Burr and Mayden 1982; Warren and Burr 1989), which were thought to have been extirpated from Illinois, were rediscovered. Examination of collections made prior to Smith's survey and recent collecting have documented previously unreported records for the bluehead shiner, *Pteronotropis hubbsi* (Burr and Warren 1986), and the pallid shiner, *Hybopsis amnis* (Warren and Burr 1988). Three fishes were recently added to the state fauna; in addition, new localities for ten other uncommon species were reported by Burr et al. (1988) and by Dimmick (1988). The introduced rainbow smelt, *Osmerus mordax*, has recently and rapidly extended its range in Illinois (Burr and Mayden 1980). The white perch, *Morone americana*, previously unrecorded from Illinois, has dispersed into the Illinois portion of Lake Michigan (Savitz et al. 1989a). The bighead carp, *Hypophthalmichthys nobilis*, silver carp, *Hypophthalmichthys molitrix*, and rudd, *Scardinius erythrophthalmus*— three Eurasian exotics unknown in Illinois streams during Smith's (1979) survey— are being captured at a number of localities, particularly big rivers and reservoirs.

My purpose here is to review briefly the Illinois fish fauna and record some of the changes that have occurred in the composition of Illinois fishes since Smith's (1979) comprehensive study. I have used the term 'alien' to encompass any fish species "of foreign origin" that is either an exotic, a transplant, or a recently invading species from more southern latitudes.

HISTORICAL PERSPECTIVE

The history of ichthyological investigations in Illinois is a rich one. At the time the Illinois Natural History Society was established in 1858, approximately three-fourths of the Illinois fish fauna had been named and described by such distinguished ichthyologists as Samuel L. Mitchill (1764–1831), Charles A. Lesueur (1778–1846), Constantine S. Rafinesque (1783–1840), Jared P. Kirtland (1793–1877), Louis Agassiz (1807–1873), and Charles F. Girard (1822–1895). Fourteen of the species described were first discovered in Illinois.

The first regional list of Illinois fishes was prepared by Robert Kennicott (1855), who treated the fishes of the Chicago area. Comprehensive catalogs of fishes of the entire state later appeared by Edward W. Nelson (1876), David Starr Jordan (1878), Stephen A. Forbes (1884), and Thomas Large (1903).

Intensive Illinois ichthyology, however, began with Stephen Forbes (1844–1930; Figure 1), the first Director of the State Laboratory of Natural History then in Normal, Illinois, and later moved to Urbana-Champaign in 1885. Sometime in the 1870s, Forbes developed the idea of producing a well-illustrated and detailed account of Illinois fishes. Year after year horse-drawn wagon parties were sent to explore and collect in different streams of the state until finally records were available for virtually every river in Illinois. The monumental effort that went into the project represented the patience and toil of 30 years. The final report, *The Fishes of Illinois*, appeared in 1908

Figure 1. Stephen Alfred Forbes (1844–1930). Photo courtesy of Illinois Natural History Survey.

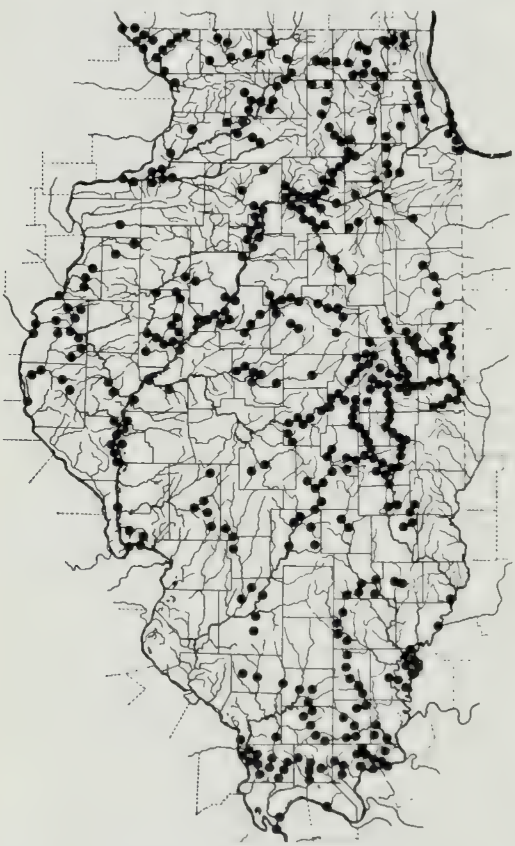

Figure 2. Location of collections of fishes made from 1876 to 1903. From Forbes and Richardson [1908].

(although no publication date is given in the volume) and was authored by Forbes and his colleague Robert Earl Richardson (1877–1935). A separate atlas of 103 range maps accompanied the volume. At that time, *The Fishes of Illinois* was considered by many to be the best regional ichthyology ever published on fishes in North America. Exceptionally skillful water colors of many species (52 in the 1908 edition, 68 in the 1920 edition), some never before published in color, were included and helped to make the book an immediate classic. Most of the copies of the initial edition were burned in a warehouse fire, and a second edition was produced in 1920.

The Forbes and Richardson data base (Figure 2) included over 200,000 fish specimens and 1,545 collections made from about 475 localities representing all major drainages and 93 of the 102 counties of Illinois. A total of 142 presently valid species (Table 1) was recorded from Illinois waters by Forbes and Richardson [1908], and only one (common carp, *Cyprinus carpio*) of those was an alien species. About 20,000 specimens used in the original *Fishes of Illinois* are vouchered in the collection of the Illinois Natural History Survey. Clearly, the superb historical data base for Illinois fishes is unique and unsurpassed by that of any other state or province in North America.

Subsequent to the masterful Forbes and Richardson treatise appeared works by Meek and Hildebrand (1910) on fishes of the Chicago region and another list of Illinois fishes by O'Donnell (1935), which added a few species to the known fauna of the state. A large number of collections made during the 1940s by Aden C. Bauman, a student of Carl L. Hubbs, contributed many significant records of Illinois fishes, particularly from the southern half of the state. Bauman's collections are at the University of Michigan Museum of Zoology and have only recently been used (Lee et al. 1980; Burr and Mayden 1982; Warren and Burr 1989).

In about 1950, Philip W. Smith (1921–1986; Figure 3), former head of one of the Illinois Natural History Survey's scientific sections and author of *The Amphibians and Reptiles of Illinois* (1961), undertook to resurvey the fishes of the state. This task provided a unique opportunity for comparing modern-day distributional data with the classic work of Forbes and Richardson. The bulk of

Smith's fieldwork began in the summer of 1962 and continued until the mid-1970s. During this period Smith published an account of the fishes of Champaign County (Larimore and Smith 1963), an annotated preliminary list of Illinois fishes (Smith 1965), an assessment of Illinois streams based on fish distribution data (Smith 1971), a key to Illinois fishes (Smith 1973), and finally, a new *Fishes of Illinois* (Smith 1979) that summarized the identification, biology, and distribution of the Illinois fish fauna.

Smith and his colleagues found 199 species in Illinois (Table 1), made over 3,000 collections from over 2,000 localities in all of the drainages of the state and in all of the 102 counties (Figure 4), and preserved as vouchers approximately 400,000 specimens deposited at the Illinois Natural History Survey. When he compared his data with those of Forbes and Richardson, Smith (1971:8) found that about 70 Illinois fishes clearly showed patterns of range decimation or extirpation from the state and that 13 alien species occupied Illinois waters.

Since the publication of Smith's (1979) treatise, state fish biologists have continued to collect data on the Illinois ichthyofauna. Particularly active have been ichthyologists and fish biologists from the state's universities, the Illinois Natural History Survey, the Illinois Department of Conservation, and several consulting firms. Additional discoveries of exotic species, native species previously unreported, and the invasion of more southerly species into Illinois waters emphasize the dynamic nature of the Illinois fauna and the need for continued collections of fishes even in presumably well-surveyed areas.

DYNAMIC NATURE OF THE ILLINOIS FAUNA

Illinois has many drainage systems and is bounded on the west by the Mississippi River, on the south by the Ohio River, on the east by the Wabash River, and on the northeast by Lake Michigan. The numerous interior streams, glacial lakes in Lake County, and cypress–tupelo swamps in southern Illinois account for the richness of the fauna. Illinois has the lowest average elevation of the north-central states. More than 90% of the state lies within the Central Lowlands Province, all of which was glaciated except the Driftless Area in extreme northwestern Illinois. Although well-watered, Illinois has lost many aquatic habitats to agriculture, stream impoundments, industrial and domestic pollution, and other modifications of watersheds.

Disappearance of Native Species

As noted previously, Smith (1971:8) documented range decimation or rarity for approximately 70 Illinois fishes; later, Smith (1979:xviii–xix) revised this number to include 52 species, some of which probably were rare even prior to European settlement. For about 120 species, no range change was detected. According to Smith (1971), several factors are primarily responsible for the disappearance of native Illinois fishes: 1) excessive siltation has caused the extinction or decimation of at least 16 species through loss of water clarity, disappearance of aquatic vegetation, and deposition of silt over rocky or sandy substrates; 2) drainage of wetlands has shrunk the ranges of at least 13 species; 3) desiccation

Table 1. Composition of Illinois fishes over the past century.

	Total no. of species	No. of aliens	No. extirpated
Forbes and Richardson [1908]	142[1] (141 native)	1	Not applicable
Smith (1979)	199 (186 native)	13	9
Present Information (1990)	209[2] (187 native)	22[3]	12[4]

[1] Forbes and Richardson [1908] recognized 150 species, 142 of which are considered valid today.
[2] Additions since Smith (1979) include Atlantic salmon, bighead carp, silver carp, rudd, taillight shiner, inland silverside, threespine stickleback, striped mullet, white perch, and Rio Grande cichlid.
[3] The number of alien species also includes three relatively recent invaders from the south (threadfin shad, inland silverside, and striped mullet); the first two of these are also stocked as forage in Illinois reservoirs.
[4] Extirpations since Smith (1979) include bluehead shiner, bigeye chub, harlequin darter, northern madtom, and alligator gar. The cypress minnow and greater redhorse, both included as extirpated by Smith (1979), have been rediscovered recently in Illinois, as noted in the text.

during drought, which has dried up once permanently flowing streams, stopped the flow in seeps and springs, and temporarily reduced the size of formerly larger rivers, has shrunk the ranges of at least 12 species; 4) interactions between species, including the effects of introduced species on native ones, competitive supplantation, and aggressive dispersal by ecologically labile species, has caused the extinction or decimation of at least 9 species; 5) industrial, domestic, and agricultural pollution has caused the decimation of at least 5 species; 6) dams and impoundments are responsible for the decimation of at least 4 species through the loss of a large variety of habitats and the blocking of natural migration; 7) higher water temperatures now than formerly, chiefly the result of stream channelization and the removal of marginal vegetation, have caused the decimation of at least 1 species. No single factor has as yet been identified for the extirpation of the muskellunge, *Esox masquinongy*, from northern Illinois or the saddleback darter, *Percina ouachitae*, from the Wabash River.

Since the publication of Smith's book (1979), the continued decline of several species has been documented. Examples include the pallid shiner, *Hybopsis amnis*, a species now known to have been much more widespread in Illinois than indicated on Smith's (1979) distribution map. It has disappeared from seven major Illinois drainages where it was known to occur from the late 1800s through the 1940s (Warren and Burr 1988). It remains in the Kankakee River drainage (Skelly and Sule 1983) and in the upper Mississippi River (Warren and Burr 1988). The Mississippi silvery minnow, *Hybognathus nuchalis*, was not taken in the recent (late 1980s) survey of the fishes of Champaign County and was rarely taken in several recent surveys in southern Illinois where suitable habitat was present. The bigeye shiner, *Notropis boops*, continues to disappear from sites of former occurrence but survives in the Little Vermilion River and the Clear Creek drainage of southern Illinois. Major impoundments (Carlyle and Shelbyville reservoirs) on the Kaskaskia River have severely limited the habitat of the western sand darter, *Etheostoma clarum*, which is now very rare (if not extinct) in the drainage. The species has, however, been taken recently in the Mississippi River below the mouth of the Missouri River (Dimmick 1988).

Figure 3. Philip Wayne Smith (1921–1986). Photo courtesy of Illinois Natural History Survey.

Figure 4. Location of collections of fishes made from 1950 to 1978. From Smith 1979.

Another striking discovery emanating from Smith's (1979) survey and subsequent work was the relatively large number of Illinois fishes that have been extirpated since the original Forbes and Richardson (1908) survey. As of this writing, these include eight species: Ohio lamprey, *Ichthyomyzon bdellium*; blackfin cisco, *Coregonus nigripinnis*; muskellunge, *Esox masquinongy*; rosefin shiner, *Lythrurus ardens*; gilt darter, *Percina evides*; saddleback darter, *Percina ouachitae*; crystal darter, *Crystallaria asprella*; and spoonhead sculpin, *Cottus ricei*.

Even more alarming is the number of species that have disappeared since Smith (1979) began his survey in the 1960s. Examples include the bluehead shiner, *Pteronotropis hubbsi*, last collected in Illinois waters in 1974 (Burr and Warren 1986) and the bigeye chub, *Hybopsis amblops*, last collected in 1961 (Smith 1979; Warren and Burr 1988). In addition, the harlequin darter, *Etheostoma histrio*, known previously from the Embarrass River, Cumberland and Jasper counties, is almost certainly extinct in Illinois, probably because of drainage alterations below Lake Charleston dam. My recent attempts (1987, 1988) to collect the northern madtom, *Noturus stigmosus*, in the Wabash drainage of Illinois have been unsuccessful. The alligator gar, *Atractosteus spatula*, has not been taken in Illinois since 1965, although sufficient effort has not been expended recently to clarify its status.

On a positive note, at least two species thought to have been extirpated at the time of Smith's (1979) survey have been rediscovered in Illinois. The cypress minnow, *Hybognathus hayi*, is now known with certainty to be reproducing in the middle Cache River drainage (and possibly in Horseshoe Lake) in southern Illinois but is still considered extirpated from former sites of occurrence in the Big Muddy River drainage (Warren and Burr 1989). The drainage of wetlands that are used as nursery areas by the species is thought to be the main factor responsible for extirpation from the Big Muddy River. The greater redhorse, *Moxostoma valenciennesi*, thought to have been extinct in Illinois since 1901, was collected in 1985 from the Illinois River, rivermile 249 (Seegert 1986) and again in 1989 from the Illinois River, rivermile 270.5. These two individuals must be part of a population residing somewhere in the upper basin.

Native Species Previously Unrecorded

One native fish has been added to the state ichthyofauna since Smith's (1979) report. The taillight shiner, *Notropis maculatus*, was discovered for the first time in Illinois in a wetland in Massac County in 1987 (Burr et al. 1988). This species was captured at only 1 of 22 wetlands sampled on the lower Wabash and Ohio rivers (Burr and Warren 1987) and should be recognized as endangered in Illinois and given highest priority for protection.

Species Expanding Their Ranges

Because the Illinois fish data base is extensive, covers two broad historical periods, and is well vouchered, it allows us to be reasonably confident of the ranges of most native, nongame fishes within the confines of Illinois. While many species have experienced range reductions in the last 90 years, a few others have expanded their ranges in response to widespread modification of habitats. An outstanding example is the red shiner, *Cyprinella lutrensis*, a species tolerant of wide fluctuations in pH, dissolved oxygen, and thermal shock (Matthews and Hill 1977). Additionally, its adaptable feeding habits and reproductive capability (Matthews and Hill 1977) in combination with its tolerance for the above-mentioned parameters undoubtedly account for its success in Illinois. This species has expanded its range north into Wisconsin, up the Ohio River drainage of southern Illinois into Kentucky and the lower Wabash River, and beginning in the 1960s crossed over from Mississippi River drainages into the upper Vermilion River drainage (Page and Smith 1970), where it has continued to move downstream to Champaign County. Another example is the silverjaw minnow, *Ericymba buccata*, which has expanded its range chiefly in the Illinois River drainage. This pioneering species quickly disperses into newly dredged ditches with sandy substrates. Because Illinois streams tend to be wider and shallower than formerly (Larimore and Smith 1963), suitable habitat for species tolerant of these conditions has increased.

Nearly all game/sport fishes and some forage species (e.g., golden shiner, *Notemigonus crysoleucas*, and fathead minnow, *Pimephales promelas*) have had their ranges expanded by numerous introductions which continue unabated in Illinois. The mosquitofish, *Gambusia affinis*, has been

widely transplanted in efforts to control mosquito outbreaks. The inland silverside, *Menidia beryllina*, was collected in 1978 from the Mississippi River at Grand Tower (a record included in a footnote by Smith [1979:211]). Beginning in 1980, this fish has been stocked as a forage species in several southern Illinois ponds and impoundments (Stoeckel and Heidinger 1989). Examples of game/sport fishes recently captured in the Illinois waters of Lake Michigan and not reported in Smith (1979) include the channel catfish, *Ictalurus punctatus*, and the black crappie, *Pomoxis nigromaculatus* (Savitz et al. 1990). Smith (1971:8) lists another five native species whose ranges have expanded in recent times.

New Records of Rare or Geographically Limited Species

Collections of Illinos fishes made during the 1940s by A.C. Bauman and those made during the 1980s have revealed new records for rare or geographically limited Illinois species that expand the information in Smith (1979). For example, the lake sturgeon, *Acipenser fulvescens*, not reported from the Mississippi River since 1966, is known from three recent records in the Mississippi (Burr et al. 1988) and Ohio rivers (Burr et al. 1990). New localities for eight other uncommon Illinois fishes were included in Burr et al. (1988). Dimmick (1988) reported the first Illinois records of the western sand darter, *Etheostoma clarum*, from the Mississippi River south of the mouth of the Missouri River; Savitz et al. (1989b) recorded the first record of the quillback, *Carpiodes cyprinus*, in the Illinois waters of Lake Michigan. Examination of voucher specimens from several U.S. museums has resulted in a reassessment of the ranges of the bigeye chub and pallid shiner (Warren and Burr 1988) as originally presented in Smith (1979).

The Alien Component and Recent Southern Invasions

Since Smith's (1979) survey, three exotics, the bighead carp, silver carp, and rudd, in addition to the four Smith reported, have been found at several localities in Illinois and, if not already established, almost certainly will be within a few years. The potential ecological effects of introduced and exotic fishes on native aquatic communities include habitat alterations (e.g., removal of vegetation, degradation of water quality); introduction of parasites and diseases; trophic alterations (e.g., predation, competition for food); hybridization; and spatial alterations (e.g., overcrowding) (Taylor et al. 1984).

Twenty-two (10.5 %) of the total of 209 fish species in Illinois are not native to the state (Table 2). Of these, at least 13 were probably intentionally introduced, 5 spread through manmade canals in the Great Lakes drainage to the Illinois portion of Lake Michigan, 1 was an unintentional introduction, and 3 euryhaline species recently invaded from more southern latitudes.

The presence of new species raises questions as to their source, their ecological role in Illinois, and their importance to human welfare. Among the 22 species, 7 are introductions from Europe or Asia; 3 are from western North America; 8 are from eastern fresh waters of the Atlantic Coast, of which 3 are introduced and 5 used canals; 3 are native to the lower Mississippi basin or Gulf Coast and have entered the state naturally or by human transfer; and 1 (the cichlid) was presumably introduced accidentally with other sport fishes. Several, probably many, additional species have in the past been introduced into Illinois waters but are not known to persist. Thousands of Atlantic salmon, *Salmo salar*, were introduced into the Mississippi River in the late 1800s (Carlander 1954). Apparently the stockings were not successful, although several individuals collected in 1986 from the Mississippi River near Chester (Burr et al. 1988) indicate that illegal stockings have apparently occurred in the river in recent decades. Grass, silver, and bighead carps have been encountered at many localities in Illinois, and the grass and bighead carps are known to be reproducing in the upper Mississippi River basin (Pflieger and Grace 1987; Pflieger 1989; Jennings 1989). A plethora of tropical and subtropical aquarium fishes have surely been released into Illinois waters (see Smith [1965] for examples) only to perish in the ensuing winter. One exception is the Rio Grande cichlid, *Cichlasoma cyanoguttatum*, released accidentally in the mid-1980s into Powerton Lake near Pekin: individuals have been observed setting up territories in that thermally treated lake during summer months (Rich Monzingo, pers. comm.). The threespine stickleback, *Gasterosteus aculeatus*, captured twice in 1988 from the Illinois portion of Lake Michigan (at Trident Harbor and Cicero), is apparently spreading rapidly through the upper Great Lakes. It was first taken in Lake Huron in

1982 (C. L. Smith 1985:276), but whether the species is self-sustaining in Illinois waters is not known.

Some of the alien species are localized geographically, rare, or small and apparently unimportant ecologically. In contrast, the salmonids, striped bass, and recently introduced carps are much valued as recreational species or for weed control, and some are common and becoming widespread. Another group of species includes the locally abundant alewife and goldfish, the widespread common carp, and the rapidly spreading rainbow smelt and white perch. These species are more or less controversial, being variously valued as sources of food or recreation but with negative ecological attributes (e.g., periodic alewife die-offs, predation, unfavorable ecological interactions with native species). The rainbow smelt, the most numerous small species in some winter seine samples from the Mississippi River for over 10 years, has not been collected from June through October and is probably not self-sustaining in the Illinois portion of the Mississippi River. The sea lamprey, an alien in Lake Michigan, has played a major role in the history and fisheries of the Great Lakes Basin.

One of the most surprising invasions in Illinois was the appearance during the fall of 1989 of the striped mullet, *Mugil cephalus*, in the Mississippi and Ohio rivers. This principally marine species had not been reported previously from Illinois waters and was known only in the published literature as far north in

Table 2. General distribution in Illinois of alien fish species and recent invaders from southern latitudes. Numbers in parentheses indicate (1) exotics introduced directly into Illinois, (2) transplants from elsewhere in North America, (3) species colonized after introduction elsewhere or through manmade access, and (4) species that have recently invaded.

Fish species by family	General distribution in Illinois
Petromyzontidae	
Petromyzon marinus, sea lamprey (3)	L. Michigan
Clupeidae	
Alosa pseudoharengus, alewife (3)	L. Michigan
Dorosoma petenense, threadfin shad (2, 4)	Ohio R., Mississippi R., Wabash R., southern Illinois reservoirs
Salmonidae	
Oncorhynchus kisutch, coho salmon (2)	L. Michigan
Oncorhynchus mykiss, rainbow trout (2)	northern half of Illinois
Oncorhynchus tshawytscha, chinook salmon (2)	L. Michigan
Salmo salar, Atlantic salmon (2)	Mississippi R.
Salmo trutta, brown trout (1)	northern Illinois, L. Michigan
Osmeridae	
Osmerus mordax, rainbow smelt (3)	L. Michigan, Illinois R., Mississippi R., Ohio R.
Cyprinidae	
Carassius auratus, goldfish (1)	Illinois and Rock R. drainage
Ctenopharyngodon idella, grass carp (1)	big rivers, reservoirs, ponds
Cyprinus carpio, common carp (1)	statewide
Hypophthalmichthys molotrix, silver carp (1)	big rivers, reservoirs, ponds
Hypophthalmichthys nobilis, bighead carp (1)	big rivers, reservoirs, ponds
Scardinius erythrophthalmus, rudd (1)	northern Illinois; sporadic
Ictaluridae	
Ameiurus catus, white catfish (2)	Illinois R., Mississippi R., Kaskaskia R.
Moronidae	
Morone americana, white perch (3)	L. Michigan
Morone saxatilis, striped bass (2)	Illinois reservoirs
Atherinidae	
Menidia beryllina, inland silverside (2, 4)	southern Illinois reservoirs, Mississippi R.
Gasterosteidae	
Gasterosteus aculeatus, threespine stickleback (3)	L. Michigan
Mugilidae	
Mugil cephalus, striped mullet (4)	Ohio R., Mississippi R.
Cichlidae	
Cichlasoma cyanoguttatum, Rio Grande cichlid (2)	Powerton L., Pekin

the Mississippi River as southern Arkansas (Robison and Buchanan 1988). According to William L. Pflieger (pers. comm.), striped mullets were obtained from the Mississippi River at New Madrid in 1983 and at Cape Girardeau in 1988. The lower water levels in the Mississippi River in 1989 may have created water quality conditions (e.g., high dissolved solids) favorable for striped mullet and allowed them to reach the upper Mississippi River basin (Burr et al. 1990).

ENDANGERED, THREATENED, AND WATCH LIST SPECIES

In the approximately 150 years since Europeans actively colonized the state of Illinois, changes in the fish fauna have been profound. Of the 187 native species (Table 1), a few have expanded their ranges and are now more abundant and more generally distributed than formerly, but many more have been decimated to some degree by the widespread modification of habitats and deterioration of water quality. Prior to the passage of the federal Endangered Species Act in 1973, attempts had been made (e.g., Lopinot and Smith 1973) to list species as rare or endangered on the basis of their natural rarity, restricted distribution, and paucity of habitat as well as on the basis of immediate or potential threats to their existence within Illinois (Smith 1979). After implementation of the act, terminology was revised to include the categories endangered and threatened. Since the longjaw ciscoe, *Coregonus alpenae*, is no longer considered a valid species and was never officially reported from the Illinois waters of Lake Michigan, none of the Illinois species qualifies as endangered (actively threatened with extinction) in the sense of the federal definition.

The Illinois Endangered Species Act of 1972 (amended in 1977) provides for some protection of rare fishes. Lists (Smith and Page 1981; Illinois Endangered Species Protection Board 1990) of endangered and threatened fishes have continued to be revised and updated; however, potential threats to rare fishes are always present and the status of each is constantly subject to change. A change in status can occur quickly, particularly in a peripheral or relict population.

Thirteen of the 187 native species are endangered and 15 are threatened (Table 3). Eleven species have been placed on a watch list (Table 4), an action that suggests they may be recategorized as endangered or threatened depending on changes that take place in Illinois. A significant concern to conservation biologists and others is the status and protection of those species that are restricted to big, free-flowing rivers (i.e., the Mississippi River). Some of the species on the watch list are big river fishes; however, because these species do not occur generally within the "inland" waters of state boundaries, they are not receiving the protection they warrant. Examples of big river fish needing more formal protection in Illinois include the pallid sturgeon, *Scaphirhynchus albus*, the flathead chub, *Platygobio gracilis*,

Table 3. Fishes categorized as endangered or threatened in Illinois according to the Illinois Endangered Species Protection Board (1990). Nomenclature has been modified where appropriate to follow Page and Burr (1991) and Warren (1989).

Endangered	Threatened
Northern brook lamprey, *Ichthyomyzon fossor*	Least brook lamprey, *Lampetra aepyptera*
Bigeye chub, *Hybopsis amblops*	Lake sturgeon, *Acipenser fulvescens*
Pallid shiner, *Hybopsis amnis*	Alligator gar, *Atractosteus spatula*
Pugnose shiner, *Notropis anogenus*	Cisco, *Coregonus artedii* (or *artedi*)
Weed shiner, *Notropis texanus*	Lake whitefish, *Coregonus clupeaformis*
Bluehead shiner, *Pteronotropis hubbsi*	Bigeye shiner, *Notropis boops*
Cypress minnow, *Hybognathus hayi*	Ironcolor shiner, *Notropis chalybaeus*
Greater redhorse, *Moxostoma valenciennesi*	Blackchin shiner, *Notropis heterodon*
Northern madtom, *Noturus stigmosus*	Blacknose shiner, *Notropis heterolepis*
Western sand darter, *Etheostoma clarum*	River redhorse, *Moxostoma carinatum*
Eastern sand darter, *Etheostoma pellucidum*	Longnose sucker, *Catostomus catostomus*
Bluebreast darter, *Etheostoma camurum*	Banded killifish, *Fundulus diaphanus*
Harlequin darter, *Etheostoma histrio*	Redspotted sunfish, *Lepomis miniatus*
	Bantam sunfish, *Lepomis symmetricus*
	Iowa darter, *Etheostoma exile*

the sturgeon chub, *Macrhybopsis gelida*, and the sicklefin chub, *Macrhybopsis meeki*. These four species are restricted in Illinois to the main channel of the Mississippi River below the mouth of the Missouri River. Intermittent sampling in the Mississippi River below the mouth of the Missouri River over a 12-year period indicates that the three chub species are naturally rare and sporadic in occurrence. Small numbers of the sicklefin chub are still being captured, but the flathead and sturgeon chubs have been taken once each since 1985. The pallid sturgeon is so rare throughout its range that it is being considered for listing as a federally endangered species.

If species that are considered extirpated from Illinois and those on the endangered, threatened, or watch lists are included, 46 species or 24% of the native fauna are experiencing trouble maintaining viable populations in Illinois. The addition of the taillight shiner, flathead chub, and sicklefin chub, which are presently not on any formal list, brings the total to 49 species or 26%.

RECOMMENDATIONS

Illinois is a model state in view of its excellent data base on fish distributions over time. Although we have learned a great deal about the effects of human activities on the aquatic environment in Illinois, we must continue to conduct basic survey work on Illinois fishes and document long-term changes in the fauna. Because fishes are sensitive indicators of environmental quality, continued collection of data will aid in monitoring a variety of stream-quality parameters and assist state agencies in identifying high-quality aquatic habitats in need of protection.

Because of the number of species extirpated or endangered in Illinois, we need to establish a monitoring program and status surveys of species on the watch list. Several of the species on the Illinois endangered list are probably already extirpated (e.g., bigeye chub, bluehead shiner) and the most effective course of action might be to allocate funds and efforts on species that may be realistically recoverable.

Over the last several years, we have come to recognize that we know comparatively little about the fundamental life histories of nongame fishes in contrast to the voluminous literature on the biology of game or sport fishes. If we are ever going to manage nongame species effectively, more funding is needed for studies on basic fish biology, especially those emphasizing reproductive biology, trophic ecology, predator-prey interactions, and parasites and diseases.

The purchase of critical habitat by The Nature Conservancy, the Illinois Department of Conservation, and other agencies has provided islands of habitat where some rare fish species can survive. For the taillight shiner, the purchase of critical habitat may be the best measure for protecting this rare and highly localized species. Several rare Illinois fishes that occur in relatively undisturbed and protected areas (e.g., LaRue–Pine Hills Swamp) continue to maintain viable populations. Efforts to purchase critical stream and wetland habitats in Illinois need to increase.

Game and sport fishes have been stocked in Illinois waters for many years. Within reason, state agencies should now consider stocking certain nongame fishes in an attempt to restore viable populations. Pond culture of endangered and threatened species should be continued in Illinois because it has provided a useful environment for studying aspects of the fundamental life histories of rare species; this information in turn leads to more effective management.

Because siltation is still considered to be the number one factor in decimation of native fish populations, we must continue to work creatively with farmers and others in protecting the valuable prairie topsoil of Illinois. The removal of gravel from headwater streams should be discouraged because the process increases erosion and destroys breeding sites of headwater creek fishes. Reservoir construction

Table 4. Fishes placed on the watch list by the Illinois Endangered Species Technical Advisory Committee on Fishes. These species do not receive protection under federal or state laws.

Pallid sturgeon, *Scaphirhynchus albus*
Round whitefish, *Prosopium cylindraceum*
Lake chub, *Couesius plumbeus*
River chub, *Nocomis micropogon*
Gravel chub, *Erimystax x-punctatus*
Sturgeon chub, *Macrhybopsis gelida*
Blacktail shiner, *Cyprinella venusta*
Northern starhead topminnow, *Fundulus dispar*
Fourhorn sculpin, *Myoxocephalus quadricornis*
Spoonhead sculpin, *Cottus ricei*
Cypress darter, *Etheostoma proeliare*

and stream channelization should also be discontinued in Illinois because of the detrimental effects these practices have on large expanses of aquatic habitat.

Finally, basic survey work on the big rivers of Illinois is badly needed. While we know comparatively little about the biology of small stream species, we know next to nothing regarding nongame, big river fishes. Unusual Illinois species (e.g., the pallid sturgeon) may disappear before we learn anything substantial about them or can protect them.

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The Aquatic Mollusca of Illinois

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Illinois has historically supported a diverse aquatic molluscan fauna, numbering over 175 species and occupying almost every type of aquatic habitat from the Great Lakes to wetlands, temporary woodland ponds, seeps, springs, and streams. Two classes of mollusks are represented in the waters of Illinois: Bivalvia, which includes the clams and mussels, and Gastropoda, represented by the snails and limpets. The native bivalves of Illinois are members of three families: the Margaritiferidae and Unionidae (the freshwater mussels) and the Sphaeriidae (the fingernail clams and peaclams). The gastropods are divided into two subclasses, Prosobranchia and Pulmonata. The Prosobranchs or the operculated, gill-breathing snails are represented in Illinois by 37 species in six families. The Pulmonates or the nonoperculated, lung-breathing snails contain 37 species in four families. A list of the species for each of the families reported from the state is given on pages 435–438. For the unionids, aspects of their biology, commercial use, and status are discussed. Information on identification, distribution, and biology of the aquatic molluscan fauna of Illinois will appear in forthcoming publications. An excellent monograph on the freshwater snails of North America has been published (Burch 1989) and should be consulted for keys and figures of most of the species found in Illinois.

The list of the freshwater mussels of Illinois (pages 435–436) is based on the examination of specimens in collections housed in the following museums: Academy of Natural Sciences, Philadelphia; Chicago Academy of Sciences; Field Museum of Natural History; Illinois Natural History Survey; Illinois State Museum; Museum of Comparative Zoology, Harvard; Ohio State University Museum of Zoology; University of Illinois Museum of Natural History; University of Michigan Museum of Zoology; and the United States National Museum. The list for Sphaeriidae and Gastropoda (pages 436–438) were compiled from the literature on Illinois Mollusca, primarily the publications of Baker (1900, 1901, 1902, 1906, 1922); Basch (1963); Burch (1989); Dexter (1956); Ulffers (1855); and Zetek (1918). Additional work is planned to verify the sphaeriid and gastropod lists by examining specimens in museum collections.

Nomenclature in this paper, with three exceptions, follows a list of common and scientific names of mollusks prepared by the Committee on Scientific and Vernacular Names of Mollusks of the Council of Systematic Malacologists, American Malacological Union (Turgeon et al. 1988). Subspecies are not recognized, nomenclature for members of the *Pleurobema cordatum* species complex follows Stansbery (1983), and nomenclature for the family Hydrobiidae follows Hershler and Thompson (1987) and Hershler et al. (1990).

The aquatic mollusks of Illinois have been studied for over 150 years. Thomas Say, the first scientist to work on mollusks in Illinois, was one of America's earliest naturalists. Say traveled to the Midwest as early as 1817 and in 1826 moved from Philadelphia to the utopian community of New Harmony, Indiana (Van Cleave 1951). While there, he collected and described many of the mollusks found in the Wabash River and its tributaries, some of which are are still recognized today.

Few attempts have been made to compile a list of the mollusk species found in Illinois. In 1906, Frank C. Baker published an annotated checklist of the Mollusca of Illinois in which he summarized the available data on the distribution of the species within the state. A prolific writer, Baker published over 400 papers, including many important works on the molluscan fauna of Illinois (Baker 1897, 1898, 1899, 1900, 1901, 1902, 1906, 1922, 1926). Baker's papers remain the best source of published information on the biology and

distribution of aquatic mollusks in the state. Other early workers on the freshwater mollusks of Illinois included Kennicott (1855); Ulffers (1855); Calkins (1874a, 1874b, 1874c); Strode (1891, 1892); Wilson and Clark (1912); Danglade (1912, 1914); Zetek (1918); and Hinkley (1919).

Few papers were published on the aquatic Mollusca of Illinois in the 1930s and 1940s. During the late 1940s and 1950s, Dr. Max R. Matteson of the University of Illinois collected mussels at over 200 sites in Illinois and amassed one of the largest and best documented collections that exists for any state in the nation. Matteson's surveys provided both distribution and abundance data on mussels from Illinois streams, many of which had not been previously sampled. His collections, now at the Illinois Natural History Survey, provide an invaluable data set and serve as the benchmark for mussel surveys conducted today.

In 1967, Paul W. Parmalee of the Illinois State Museum published *The Fresh-water Mussels of Illinois*, which included many original observations on the distribution and habitat of unionids. This monograph, one of the most frequently cited regional works on freshwater mussels, is still the best guide available on the mussels of the state. Other papers on aquatic mollusks of Illinois in the 1950s and 60s include van der Schalie and van der Schalie (1950); Dexter (1953, 1956); Parmalee (1955, 1956); Matteson (1961); Matteson and Dexter (1966); and Fechtner (1963).

In the 1970s and 1980s, stream surveys were conducted on the Illinois (Starrett 1971), Kankakee (Lewis and Brice 1980; Suloway 1981), Kaskaskia (Suloway et al. 1981), and Wabash rivers (Meyer 1974; Clark 1976). These and current studies document the rapid decline of the freshwater mussels of Illinois and provide data on the status of rare species.

BIVALVIA: MUSSELS AND CLAMS

Freshwater mussels in the families Margaritiferidae and Unionidae are found throughout the holarctic region but reach their greatest diversity in eastern North America, where they number about 285 species (Turgeon et al. 1988). A total of 78 species in two families and four subfamilies has been recorded from Illinois and boundary waters (pages 435–436).

Biology. Mussels filter-feed on plankton, which they remove from the water as it circulates through the animal via incurrent and excurrent aperatures. In most freshwater mussel species, the sexes are separate. Sperm are released into the water and taken into the female via the incurrent aperature. The eggs are fertilized and develop into an intermediate stage, the glochidium. Glochidia are stored in the female's gills, which function as brood chambers. Nearly all unionids must pass through a parasitic phase in order to complete their life cycle. In the spring or summer, glochidia are expelled into the water and must come in contact with the appropriate host, usually a fish, to which they attach and metamorphose into a juvenile mussel. Glochidia are either internal parasites on the gills or external parasites on the fins. Some species are host specific, but others are generalists and use a wide variety of fishes as hosts. Mussels are long lived. Many species live as long as 25 years, and some are reported to live more than 50 years.

Commercial Use. In 1891 a German immigrant, J.F. Boepple of Petersburg, Illinois, realized that the mussels of the United States could be used, as they had been in Europe, to manufacture buttons. In the early part of the twentieth century, enormous quantities of mussels were harvested for the button industry, with some beds in Illinois producing over 700 tons in a single year (Coker 1919). Mussel shells were collected, cooked out, and shipped to factories where they were cut into blanks, sorted, polished, and finished into buttons. Today freshwater mussel shells are exported to Japan where they are converted into beads and inserted into oysters where they serve as nuclei for cultured pearls. The oysters are maintained in cages under water, and over a period of about a year, a layer of mother-of-pearl is secreted around the bead to form the pearl.

From 1912 to 1914, roughly 15,000 tons of shells were taken in Illinois and boundary waters and sold at a price that varied from \$4 to \$10 a ton. The increase in price over the last 75 years has been astronomical. In the 1940s, the price of shells was about \$25 a ton and remained at that level until the button industry collapsed in the late 1950s due to the advent of plastics. As the demand for shells to manufacture cultured pearls increased, so did the price, from \$45 a ton in the 60s, \$800 in the 70s, and

$1,800 in the 80s, to $2,400 a ton this year (N. Cohen, pers. comm.). At current prices, the estimated harvest of 1912 to 1914 would be worth about $36 million.

Status. Surveys across North America have documented significant declines in freshwater mussel populations. Recent surveys for mussels in Illinois using the same methods as those of previous studies have documented a reduction in the fauna for all streams sampled (Table 1). In 1966, William C. Starrett of the Illinois Natural History Survey conducted an in-depth study of the Illinois River. He collected only 23 of the 47 species previously reported from the Illinois (Starrett 1971). Two of the 24 extirpated species were the butterfly, *Ellipsaria lineolata* (Rafinesque 1820), a species that has declined statewide in recent years; and the Higgins eye, *Lampsilis higginsi* (Lea 1857), now on the federally endangered species list. Similar results were obtained in the Kankakee River where Suloway (1981) reported only 24 of the 32 species historically known to inhabit the river. The Kankakee River drainage continues to support some of the richest mussel populations of the state, including the state threatened bullhead, *Plethobasus cyphyus* (Rafinesque 1820), and the ellipse, *Venustaconcha ellipsiformis* (Conrad 1836). In the Kaskaskia River, the decline in diversity has been pronounced. Only 32 of the 39 species recorded from the drainage were found in 1956, and that number was reduced to 24 by 1978 (Suloway et al. 1981). In addition, the number of individuals dropped from 2,595 to 498, an 80% reduction in just over 20 years. A survey of the Sangamon River in 1988–1989 recovered all of the species found in 1956–1960; however, overall numbers collected per unit of effort were much lower, and some, for example, *Elliptio dilatata* (Rafinesque 1820) and *Megalonaias nervosa* (Rafinesque 1820) have been nearly extirpated (Schanzle and Cummings 1991).

Table 1. Selected streams in Illinois where recent surveys have documented declines in the freshwater mussel fauna. Data from Starrett 1971; Suloway et al. 1981; Suloway 1981; and Cummings et al. unpublished.

	Number of mussel species	
	Pre-1960	Post-1960
Mississippi River drainage		
Illinois River	47	23
Kaskaskia River	39	24
Kankakee River	32	24
Wabash River drainage		
Embarras River	44	27
Vermilion River	41	25
Little Wabash River	41	31

In the Wabash River drainage, even the relatively undisturbed Vermilion River has suffered a serious decline, with almost 40% of the mussel species extirpated by the 1970s. Although its species richness has declined, this river supports the only known populations of at least two state endangered species: the wavy-rayed lampmussel, *Lampsilis fasciola* Rafinesque 1820, and the rabbitsfoot, *Quadrula cylindrica* (Say 1817). The pattern is the same in the Embarras River, where the number of species has dropped from 44 to 27. A comparison of surveys done in 1956 and 1986 revealed that the Embarras River continues to support a fairly diverse fauna; however, the number of individuals has declined over 80% in the last 30 years. Two state endangered species are found in Illinois only in the Embarras: the kidneyshell, *Ptychobranchus fasciolaris* (Rafinesque 1820), and the snuffbox, *Epioblasma triquetra* (Rafinesque 1820). The Little Wabash River has suffered a similar decline, and a 1988 survey revealed that only 31 of the 41 species known to have occurred in the drainage are extant.

A variety of factors are responsible for the decline of mussel populations. Foremost is siltation from agricultural run-off due to poor land management. Mussels are sedentary and particularly susceptible to the smothering effects of siltation. Channelization is detrimental because it eliminates habitat for mussels as well as potential host fishes. Impoundments often create good habitat directly below the dam, but they also inundate large areas of the stream and impede the migration of host species. Herbicides, pesticides, and petroleum-related pollution also have negative effects, and competition from exotics has been implicated in the decline of native mussels, although the mechanisms involved are not entirely understood.

One result of the status surveys conducted in Illinois and other states in recent years has been the addition of many mussel species to state and federally endangered species lists. Thirteen species are now consid-

ered to be globally extinct, including four once found in Illinois (Turgeon et al. 1988; see listing on pages 435–436, this publication). On the federal level, 37 mussels are listed as endangered and another 56 are proposed or candidates for listing (U.S. Department of the Interior, Fish and Wildlife Service 1989a, 1989b). The Illinois Threatened and Endangered Species List now contains 33 mussels (29 endangered and 4 threatened), slightly over 40% of the species ever recorded from Illinois (Illinois Endangered Species Protection Board 1990). Another 11 species are candidates or species of special concern that may be listed in the future. These bring the total number of rare, endangered, or extirpated species in Illinois to 44 species—56% of the state's known mussel fauna. Other states have similar problems. North Carolina, for example, recently reported that half of its mussel species are disappearing and in need of protection (Venters 1990). This national decline has received some much needed attention and funding has been provided in recent years to begin to document and address the problem.

The fingernail clams and peaclams of the family Sphaeriidae are holarctic in distribution and occupy a wide variety of habitats. Thirty-eight species in four genera are found in North America, and 26 species in three genera are reported from Illinois (pages 436–437). Although little has been published on the distribution and status of these animals in Illinois since Baker's list of 1906, unpublished reports make clear that many species have disappeared from the streams in which they formerly occurred and are declining throughout their range. Sphaeriids are hermaphroditic and, unlike freshwater mussels, have direct development, with about 2 to 20 young produced per female. Although sphaeriids have no direct economic value, they are an important food source for many animals, including fishes and diving ducks.

The family Corbiculidae is represented in Illinois by the exotic Asian Clam, *Corbicula fluminea* (Müller 1774). Introduced in North American in the 1920s (Counts 1981), this species was first reported in Illinois from the Ohio River in southern Illinois in the early 1960s (Fechtner 1962). Since then it has spread at least as far north as Rock Island and is present in most if not all drainages in the state. As is the case with most established exotics, *Corbicula* has had serious negative effects on the environment. This extremely prolific clam has caused major problems associated with the fouling of cooling water intakes of power plants (Isom 1986) and may outcompete native species (Clarke 1988).

The family Dreissenidae is represented in North American freshwaters by the zebra mussel *Dreissena polymorpha* (Pallas 1771). Although the zebra mussel is not currently established in Illinois waters, it was recently discovered in the Indiana portion of Lake Michigan and its arrival here is imminent. This exotic is causing tremendous economic problems in Lake Erie and Lake St. Clair and will negatively affect our native mussels by smothering and suffocating them as it has in the Great Lakes.

GASTROPODA: FRESHWATER SNAILS

Freshwater snails are basically herbivores and detritivores and use their radulae to scrape algae and diatoms from plants and rocks. About 500 species of freshwater snails are found in North America, 350 Prosobranchs and 150 Pulmonates (Burch 1989). Of those, 85 or about one-fifth of the species are candidates for federal protection (U.S. Department of Interior, Fish and Wildlife Service 1989b). A review of the literature suggests that there are or were about 74 species of freshwater snails in Illinois, two of which were introduced and three that are under consideration for federal listing (pages 437–438).

The subclass Prosobranchia is represented in Illinois by 37 species in six families: Valvatidae, Viviparide, Bithyniidae, Hydrobiidae, Pomatiopsidae, and Pleuroceridae.

The shells of North American Valvatidae are relatively small (up to 5 mm) and flattened in shape. Valvatids are egg layers and, unlike most Prosobranchs, hermaphroditic. Five species, all in the genus *Valvata*, have been reported from Illinois.

The family Viviparidae is found on all continents except Antarctica and South America and occurs throughout eastern North America. The sexes are separate, and as their name implies, they are "live bearers" as opposed to egg layers. Six species in three genera are found in Illinois.

The family Bithyniidae is represented in Illinois by the Mud Bithynia, *Bithynia tentaculata* (Linnaeus 1758). This species also occurs in Europe, and populations have been introduced into North America where the species has spread widely (Burch 1989). *Bithynia tentaculata* has been reported from Pleistocene deposits in Chicago, and it may, therefore, have been present in North America before Europeans arrived.

The family Hydrobiidae is one of the most common and widely distributed snail families in the world. These small- to medium-sized snails are a major component of the North American fauna and number about 35 genera and 170 species (Hershler and Thompson 1987; Turgeon et al. 1988). Most live in fresh water, although a few have been found in brackish water. Twelve species in seven genera have been reported from Illinois.

The family Pomatiopsidae is represented in North America by six species, two of which are found in Illinois. These snails are usually regarded as amphibious, inhabiting river banks or moist areas near streams.

The Pleuroceridae are widely distributed, occurring in North, Central, and South America and in Africa and Asia. They reach their greatest diversity, however, in the southeastern United States. Pleurocerids are extremely sensitive to the effects of pollution and siltation. At least 23 species are presumed extinct, and many others are candidates for threatened or endangered status (Turgeon et al. 1988; U.S. Department of the Interior, Fish and Wildlife Service 1989b). Eleven species in four genera have been found in Illinois, three of which are candidates for federal listing (page 437). Their current status in Illinois is unknown and needs investigation.

The subclass Pulmonata is represented in Illinois by four families. Like the pleurocerids, members of the family Lymnaeidae are found worldwide but reach their greatest diversity in North America. Fourteen species (1 introduced) in six genera have been reported from Illinois.

The family Physidae is mainly a New World family with a few species found in Eurasia and Africa. Physids are found in a wide variety of habitats and are the most widespread and abundant snails in North America. They appear to be the most pollution tolerant of all freshwater mollusks and may be the only species found in highly degraded waters.

The family Planorbidae is restricted to fresh water and is worldwide in distribution. Planorbids vary widely in size from about 1 to 30 mm. A few species are known to serve as intermediate hosts for human parasites and have been studied extensively; most others are relatively unknown ecologically. Twelve species (1 introduced) in six genera have been found in Illinois.

The Ancylidae, or freshwater limpets, are worldwide in distribution and are found in many freshwater habitats. The family, revised in 1963, is currently thought to contain about 13 species in four genera (Basch 1963; Turgeon et al. 1988). Ancylids can usually be found attached to aquatic vegetation or living on stones or other debris. Little is known about the biology of freshwater limpets, but they are reported to be fairly intolerant of chemical pollution (Basch 1963). Six species in three genera have been found in Illinois.

The current distribution and status of gastropods in Illinois are poorly understood, and as a result we are unable to compile a list of threatened or endangered freshwater snail species for the state. Given the documented decline in freshwater mussels and other aquatic organisms, however, there can be little doubt that Illinois has lost and is likely in danger of losing many species of snails as well.

Conservation efforts in Illinois and other states have thus far concentrated on preserving or protecting terrestrial ecosystems and their inhabitants. While the protection of prairies, bogs, fens, glades, and forests is an extremely important and worthwhile endeavor, we need to protect aquatic habitats as well or we will most certainly lose many of the fascinating and unique species that are found in the fresh waters of North America.

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The Aquatic Mollusca of Illinois. Species are arranged alphabetically within each family or in the case of Unionidae within each subfamily. Abbreviations for status are as follows: (†) = extinct, X = extirpated from Illinois, FE = federally endangered, FC = federal candidate, SE = state endangered, ST = state threatened, SC = state candidate (watch list), I = introduced.

Scientific Name	Common Name	Status[1]
CLASS BIVALVIA		
ORDER UNIONOIDA		
Family Margaritiferidae (1 species)		
Subfamily Cumberlandinae		
Cumberlandia monodonta (Say 1829)	Spectaclecase	FC, SE
Family Unionidae (77 species)		
Subfamily Ambleminae		
Amblema plicata (Say 1817)	Threeridge	
Cyclonaias tuberculata (Rafinesque 1820)	Purple wartyback	
Elliptio crassidens (Lamarck 1819)	Elephant-ear	ST
Elliptio dilatata (Rafinesque 1820)	Spike	SC
Fusconaia ebena (Lea 1831)	Ebonyshell	SC
Fusconaia flava (Rafinesque 1820)	Wabash pigtoe	
Fusconaia subrotunda (Lea 1831)	Long-solid	FC, SC, X
Hemistena lata (Rafinesque 1820)	Cracking pearlymussel	FE, SE, X
Megalonaias nervosa (Rafinesque 1820)	Washboard	
Plethobasus cicatricosus (Say 1829)	White wartyback	FE, SE, X
Plethobasus cooperianus (Lea 1834)	Orange-foot pimpleback	FE, SE
Plethobasus cyphyus (Rafinesque 1820)	Sheepnose	ST
Pleurobema clava (Lamarck 1819)	Clubshell	FC, SE
Pleurobema cordatum (Rafinesque 1820)	Ohio pigtoe	SC
Pleurobema plenum (Lea 1840)	Rough pigtoe	FE, SE, X
Pleurobema rubrum (Rafinesque 1820)	Pyramid pigtoe	SC
Pleurobema sintoxia (Rafinesque 1820)	Round pigtoe	
Quadrula cylindrica (Say 1817)	Rabbitsfoot	SE
Quadrula fragosa (Conrad 1835)	Winged mapleleaf	FC, SC, X
Quadrula metanevra (Rafinesque 1820)	Monkeyface	
Quadrula nodulata (Rafinesque 1820)	Wartyback	
Quadrula pustulosa (Lea 1831)	Pimpleback	
Quadrula quadrula (Rafinesque 1820)	Mapleleaf	
Tritogonia verrucosa (Rafinesque 1820)	Pistolgrip	
Uniomerus tetralasmus (Say 1831)	Pondhorn	ST
Subfamily Anodontinae		
Alasmidonta marginata Say 1818	Elktoe	
Alasmidonta viridis (Rafinesque 1820)	Slippershell	SE
Anodonta grandis Say 1829	Giant floater	
Anodonta imbecillis Say 1829	Paper pondshell	
Anodonta suborbiculata Say 1831	Flat floater	
Anodontoides ferussacianus (Lea 1834)	Cylindrical papershell	
Arcidens confragosus (Say 1829)	Rock-pocketbook	
Lasmigona complanata (Barnes 1823)	White heelsplitter	
Lasmigona compressa (Lea 1829)	Creek heelsplitter	ST
Lasmigona costata (Rafinesque 1820)	Fluted-shell	
Simpsonaias ambigua (Say 1825)	Salamander mussel	FC, SE
Strophitus undulatus (Say 1817)	Squawfoot	
Subfamily Lampsilinae		
Actinonaias ligamentina (Lamarck 1819)	Mucket	
Cyprogenia stegaria (Rafinesque 1820)	Fanshell	FE, SE
Ellipsaria lineolata (Rafinesque 1820)	Butterfly	SC
Epioblasma flexuosa (Rafinesque 1820)	Leafshell	(†), SE, X
Epioblasma obliquata (Rafinesque 1820)	Catspaw	FE, SE, X.
Epioblasma personata (Say 1829)	Round combshell	(†), SE, X

Scientific Name	Common Name	Status[1]
Epioblasma propinqua (Lea 1857)	Tennessee riffleshell	(†), SE, X
Epioblasma rangiana (Lea 1839)	Northern riffleshell	FC, SC, X
Epioblasma sampsonii (Lea 1861)	Wabash riffleshell	(†), SE, X
Epioblasma torulosa (Rafinesque 1820)	Tubercled blossom	FE, SE, X
Epioblasma triquetra (Rafinesque 1820)	Snuffbox	SE
Lampsilis abrupta (Say 1831)	Pink mucket	FE, SE, X
Lampsilis cardium Rafinesque 1820	Plain pocketbook	
Lampsilis fasciola Rafinesque 1820	Wavy-rayed lampmussel	SE
Lampsilis higginsi (Lea 1857)	Higgins eye	FE, SE
Lampsilis ovata (Say 1817)	Pocketbook	SC
Lampsilis siliquoidea (Barnes 1823)	Fatmucket	
Lampsilis teres (Rafinesque 1820)	Yellow sandshell	
Leptodea fragilis (Rafinesque 1820)	Fragile papershell	
Leptodea leptodon (Rafinesque 1820)	Scaleshell	FC, SE, X
Ligumia recta (Lamarck 1819)	Black sandshell	
Ligumia subrostrata (Say 1831)	Pondmussel	
Obliquaria reflexa Rafinesque 1820	Threehorn wartyback	
Obovaria olivaria (Rafinesque 1820)	Hickorynut	
Obovaria retusa (Lamarck 1819)	Ring Pink	FE, SE, X
Obovaria subrotunda (Rafinesque 1820)	Round hickorynut	SE
Potamilus alatus (Say 1817)	Pink heelsplitter	
Potamilus capax (Green 1832)	Fat pocketbook	FE, SE
Potamilus ohiensis (Rafinesque 1820)	Pink papershell	
Potamilus purpuratus (Lamarck 1819)	Bleufer	SC
Ptychobranchus fasciolaris (Rafinesque 1820)	Kidneyshell	SE
Toxolasma lividus (Rafinesque 1831)	Purple lilliput	FC, SE
Toxolasma parvus (Barnes 1823)	Lilliput	
Toxolasma texasensis (Lea 1857)	Texas lilliput	
Truncilla donaciformis (Lea 1828)	Fawnsfoot	
Truncilla truncata Rafinesque 1820	Deertoe	
Venustaconcha ellipsiformis (Conrad 1836)	Ellipse	SC
Villosa fabalis (Lea 1831)	Rayed bean	FC, SE, X
Villosa iris (Lea 1829)	Rainbow	SE
Villosa lienosa (Conrad 1834)	Little spectaclecase	SE
ORDER VENEROIDA		
Family Sphaeriidae (26 species)		
Musculium lacustre (Müller 1774)	Lake fingernailclam	
Musculium partumeium (Say 1822)	Swamp fingernailclam	
Musculium securis (Prime 1852)	Pond fingernailclam	
Musculium transversum (Say 1829)	Long fingernailclam	
Pisidium adamsi Prime 1851	Adam peaclam	
Pisidium casertanum (Poli 1791)	Ubiquitous peaclam	
Pisidium compressum Prime 1852	Ridged-beak peaclam	
Pisidium conventus Clessin 1877	Alpine peaclam	
Pisidium cruciatum Sterki 1895	Ornamented peaclam	
Pisidium dubium (Say 1817)	Greater eastern peaclam	
Pisidium equilaterale Prime 1852	Round peaclam	
Pisidium fallax Sterki 1896	River peaclam	
Pisidium ferrugineum Prime 1852	Rusty peaclam	
Pisidium idahoense Roper 1890	Giant northern peaclam	
Pisidium lilljeborgi (Clessin 1886)	Lilljeborg peaclam	
Pisidium nitidum Jenyns 1832	Shiny peaclam	
Pisidium punctatum Sterki 1895	Perforated peaclam	
Pisidium punctiferum (Guppy 1867)	Striate peaclam	
Pisidium rotundatum Prime 1852	Fat peaclam	
Pisidium variabile Prime 1852	Triangular peaclam	
Pisidium walkeri Sterki 1895	Walker peaclam	
Sphaerium fabale (Prime 1852)	River fingernailclam	

Scientific Name	Common Name	Status[1]
Sphaerium occidentale (Lewis 1856)	Herrington fingernailclam	
Sphaerium rhomboideum (Say 1822)	Rhomboid fingernailclam	
Sphaerium simile (Say 1817)	Grooved fingernailclam	
Sphaerium striatinum (Lamarck 1818)	Striated fingernailclam	
Family Corbiculidae (1 species)		
Corbicula fluminea (Müller 1774)	Asian clam	I
Family Dreissenidae (1 species)		
Dreissena polymorpha (Pallas 1771)	Zebra mussel	I
CLASS GASTROPODA (74 species)		
SUBCLASS PROSOBRANCHIA		
ORDER MESOGASTROPODA		
Family Valvatidae (5 species)		
Valvata bicarinata Lea 1841	Two-ridge valvata	
Valvata lewisi Currier 1868	Fringed valvata	
Valvata perdepressa Walker 1906	Purplecap valvata	
Valvata sincera Say 1824	Mossy valvata	
Valvata tricarinata (Say 1817)	Threeridge valvata	
Family Viviparidae (6 species)		
Campeloma crassulum Rafinesque 1819	Ponderous campeloma	
Campeloma decisum (Say 1817)	Pointed campeloma	
Lioplax sulculosa (Menke 1827)	Furrowed lioplax	
Viviparus georgianus (Lea 1834)	Banded mysterysnail	
Viviparus intertextus (Say 1829)	Rotund mysterysnail	
Viviparus subpurpureus (Say 1829)	Olive mysterysnail	
Family Bithyniidae (1 species)		
Bithynia tentaculata (Linnaeus 1758)	Mud bithynia	
Family Hydrobiidae (12 species)		
Amnicola limosa (Say 1817)	Mud amnicola	
Amnicola pilsbryi Walker 1906	Lake duskysnail	
Amnicola walkeri Pilsbry 1898	Canadian duskysnail	
Birgella subglobosus (Say 1825)	Globe siltsnail	
Fontigens aldrichi (Call & Beecher 1886)	Hoosier amnicola	
Fontigens antroecetes (Hubricht 1940)		
Fontigens nickliniana (Lea 1838)	Watercress snail	
Hoyia sheldoni (Pilsbry 1890)	Storm hydrobe	
Probythinella lacustris (Baker 1928)	Delta hydrobe	
Pyrgulopsis lustrica (Pilsbry 1890)	Boreal marstonia	
Pyrgulopsis scalariformis (Wolf 1870)	Moss pyrg	
Somatogyrus depressus (Tryon 1862)	Sandbar pebblesnail	
Family Pomatiopsidae (2 species)		
Pomatiopsis cincinnatiensis (Lea 1840)	Brown walker	
Pomatiopsis lapidaria (Say 1817)	Slender walker	
Family Pleuroceridae (11 species)		
Elimia costifera (Reeve 1861)	Corded elimia	
Elimia livescens (Menke 1830)	Liver elimia	
Elimia semicarinata (Say 1829)	Fine-ridged elimia	
Leptoxis praerosa (Say 1821)	Onyx rocksnail	FC, SC
Leptoxis trilineata (Say 1829)	Broad mudalia	
Lithasia armigera (Say 1821)	Armored rocksnail	FC, SC
Lithasia obovata (Say 1829)	Shawnee rocksnail	
Lithasia verrucosa (Rafinesque 1820)	Verrucose rocksnail	FC, SC
Pleurocera acuta Rafinesque 1831	Sharp hornsnail	
Pleurocera alveare (Conrad 1834)	Rugged hornsnail	
Pleurocera canaliculata (Say 1821)	Silty hornsnail	

Scientific Name	Common Name	Status [1]
SUBCLASS PULMONATA		
ORDER BASOMMATOPHORA		
Family Lymnaeidae (14 species)		
Acella haldemani (Binney 1867)	Spindle lymnaea	
Fossaria dalli (Baker 1907)	Dusky fossaria	
Fossaria humilis (Say 1822)	Marsh fossaria	
Fossaria obrussa (Say 1825)	Golden fossaria	
Fossaria parva (Lea 1841)	Pygmy fossaria	
Fossaria tazewelliana (Wolf 1870)	Tazewell fossaria	
Lymnaea stagnalis Linnaeus 1758	Swamp lymnaea	
Pseudosuccinea columella (Say 1817)	Mimic lymnaea	
Radix auricularia (Linnaeus 1758)	Big-ear radix	I
Stagnicola caperatus (Say 1829)	Wrinkled marshsnail	
Stagnicola catascopium (Say 1817)	Woodland pondsnail	
Stagnicola elodes (Say 1821)	Marsh pondsnail	
Stagnicola exilis (Lea 1834)	Flat-whorled pondsnail	
Stagnicola woodruffi (Baker 1901)	Coldwater pondsnail	
Family Physidae (5 species)		
Aplexa elongata (Say 1821)	Lance aplexa	
Physella gyrina (Say 1821)	Tadpole physa	
Physella heterostropha (Say 1817)	Pewter physa	
Physella integra (Haldeman 1841)	Ashy physa	
Physella virgata (Gould 1855)	Protean physa	
Family Planorbidae (12 species)		
Biomphalaria glabrata (Say 1818)	Bloodfluke planorb	I
Gyraulus deflectus (Say 1824)	Flexed gyro	
Gyraulus parvus (Say 1817)	Ash gyro	
Helisoma anceps (Menke 1830)	Two-ridge rams-horn	
Micromenetus dilatatus (Gould 1841)	Bugle sprite	
Micromenetus sampsoni (Ancey 1885)		
Planorbella armigera (Say 1821)	Thicklip rams-horn	
Planorbella campanulata (Say 1821)	Bellmouth rams-horn	
Planorbella pseudotrivolvis (Baker 1920)		
Planorbella trivolvis (Say 1817)	Marsh rams-horn	
Planorbella truncata (Miles 1861)	Druid rams-horn	
Promenetus exacuous (Say 1821)	Sharp sprite	
Family Ancylidae (6 species)		
Ferrissia fragilis (Tryon 1863)	Fragile ancylid	
Ferrissia parallela (Haldeman 1841)	Oblong ancylid	
Ferrissia rivularis (Say 1817)	Creeping ancylid	
Laevapex diaphanus (Haldeman 1841)	Cymbal ancylid	
Laevapex fuscus (Adams 1840)	Dusky ancylid	
Rhodacmea hinkleyi (Walker 1908)	Knobby ancylid	

[1] Readers may be puzzled by such dual designations for a species as endangered and extirpated or endangered and extinct The current Illinois list of threatened and endangered mussels was compiled in 1987. Since that time, surveys have determined that some of the species on that list are probably no longer extant Future lists will reflect such changes and species thought to be extirpated or extinct will be removed. At the present time, however, a species may continue to be listed as endangered but considered by researchers to be extirpated or extinct.

Streams of Illinois

Lawrence M. Page, Illinois Natural History Survey

The recent increased interest in protecting streams (Phillippi and Anderson 1989) is an extremely welcome development. Until now, little effort has been directed toward protecting flowing bodies of water in Illinois, largely because of the difficulties of the task. In contrast, completion of a natural areas inventory in Illinois and excellent efforts by the Illinois Nature Preserves Commission and The Nature Conservancy have resulted in safeguarding a number of prairies and other terrestrial ecosystems.

To protect our streams, we need to gather data and develop appropriate methodologies. To organize this process, we need to address the following questions in relation to streams: What does Illinois have? What should we protect? What are the major causes of stream degradation? How do we protect streams?

WHAT DOES ILLINOIS HAVE?

Because Illinois has a large and complex drainage pattern (Figure 1), it is considered a well-watered state, particularly in relation to most western states. It is bounded on the west by the Mississippi River, on the south by the Ohio, on the northeast by Lake Michigan, and on the southeast by the Wabash. An excellent discussion of the drainages of Illinois and their characteristics at the turn of the century was undertaken by C.W. Rolfe in Forbes and Richardson's *The Fishes of Illinois* [1908]. The biogeography of the fishes of Illinois and other states of the lower Ohio and upper Mississippi River basins is discussed by Burr and Page (1986).

The geological characteristics of Illinois strongly influence the diversity and distributions of its aquatic biota, and the streams of Illinois can be classified physiographically according to Fenneman's physiographic provinces (Fenneman 1938):

I. Great Lakes: Lake Michigan Section
II. Mississippi River
- A. Wisconsin Driftless Section
- B. Till Plains Section
  1. Wisconsin Glacial Till
  2. Illinoian Glacial Till
- C. Shawnee Hills–Ozark Plateaus Section
- D. Coastal Plain Section

The streams over most of Illinois are relatively recent products of glaciation. Those flowing into Lake Michigan and those on the Till Plains Section developed after Pleistocene glaciers had receded and are less than 100,000 years old; those north of the Shelbyville moraine, the southern terminus of the Wisconsin glaciation, are less than 10,000 years old. In contrast, streams in the unglaciated areas of Illinois—the Wisconsin Driftless, Shawnee Hills, and Coastal Plain sections—traverse much older areas. Unglaciated areas exhibit more topographic relief and have more bedrock; their streams are characterized by higher gradients, and they often sustain unique aquatic communities.

The Illinois portion of the Wisconsin Driftless Section is found mostly in Jo Daviess County. It escaped glaciation, and the streams there are the product of millions of years of geological evolution. Relict populations of species otherwise eliminated from Illinois by the glaciers (e.g., the Ozark minnow, *Notropis nubilus*) remain there. The major stream of the area is the Apple River.

The Till Plains Section is the vast area of the state covered during the Pleistocene by one or more glacial advances. During glaciation, old river channels were filled with glacial drift. As the glaciers receded, drift was laid down in ridges that acted as dams holding back meltwater and creating large lakes. Later, over long periods of time, the lakes filled with depositional materials, drainage outlets formed in the moraines, and the lakes transformed into marshes and prairies. Water flowing through

the marshes and prairies eventually cut the drainage patterns that exist today. Nearly the entire region covered by glacial till (Till Plains Section) is drained by tributaries flowing southwest into the Mississippi River (mainly, the Rock, Illinois, Kaskaskia, and Big Muddy rivers) and by tributaries flowing southeast into the Wabash and Ohio rivers (the Vermilion, Embarras, Little Wabash, and Saline rivers).

The Shawnee Hills are composed almost entirely of Mississippian limestone and sandstone and stand an average of about 400 feet above the surrounding land. Several of the most interesting streams and aquatic organisms, including species endemic to Illinois, such as the Illinois crayfish (*Orconectes illinoiensis*), occur in this region. The streams of the Shawnee Hills—including Big, Lusk (Figure 2), Big Grand Pierre, and Clear creeks—are small, clear rocky streams that are among the most scenic in the state.

The Coastal Plain lies south of the Shawnee Hills. Flat, sandy, and covered by residual soils, it is drained almost entirely by the Cache River and small tributaries of the Ohio. Aquatic organisms found on the Illinois Coastal Plain tend to be restricted to this region in Illinois, although they are also characteristic of the Coastal Plain to the south of Illinois. Because the Illinois portion of the Coastal Plain is small, many species found there are rare and restricted and therefore protected in Illinois.

The present character of the streams of Illinois is as much a function of human activities as it is of the evolution of drainage patterns. What we have done to the streams in the last 200 years has had a major impact on the distributional patterns and community structure established during the millions of years of geological history that preceded our arrival. The questions now are, what does Illinois have left and what should be protected and from what?

Figure 1. Major streams of Illinois.

Figure 2. Lusk Creek Canyon, Pope County, Illinois. Photo by Michael Jeffords.

WHAT SHOULD WE PROTECT?

An element of scenic beauty apart from living organisms is certainly worth preserving, but generally we are interested in protecting life. In deciding what to protect, we can concentrate on biodiversity. The species that remain are of interest and of value to us for a number of reasons, and it seems clear that we as a society, through the establishment of environmental protection agencies and endangered species lists, have stated emphatically that we want to protect them. The reasons for protecting species include vital as well as aesthetic and economic considerations. Living organisms provide the oxygen we breathe and the food we eat and are the source of many of our medicines. We enjoy the beauty and diversity of life and acknowledge that our lives without wild places and wild plants and animals would be much less interesting and enjoyable. By maintaining a diversity of plants and animals, we are also maintaining a variety of choices for the biological control of noxious species; surely that option is more likely to result in a healthy environment than is resorting to potentially dangerous pesticides.

Because of the enormous modifications of the Illinois landscape, we are faced with protecting large numbers of species. Our present list of endangered and threatened animals and plants includes nearly 500 species. In addition to these, which are considered to be in risk of extirpation from the state, thousands of others have disappeared or declined significantly in abundance in the past 200 years. In a sense, because Illinois is so highly modified, we are faced with protecting almost all native species. Unfortunately, it is too late to protect complete watersheds and other large areas (the exception being Heron Pond–Little Black Slough Preserve in southern Illinois), and thus we need to concentrate on identifying and protecting streams with high species diversity and those with rare species. Other parameters that might be used to select streams to protect, for example, water quality, land use, unusual habitats, naturalness of the ecosystem, and natural divisions, are reflected in the biodiversity. If many species or rare species are present, it is because the water quality has remained good for a long time, because unusual habitats are present, and so on.

How do we recognize streams with high diversity and rare diversity? The best way is to obtain data from large geographic, in this instance statewide, data bases and compare various localities with one another. Fortunately, Illinois has more complete statewide data bases on the diversity of aquatic organisms than any other state. Burr (pages 417–427, this volume) has discussed the surveys of fishes (Forbes and Richardson [1908]; Smith 1979), and Cummings (pages 428–438, this volume) has discussed past (Parmalee 1967; Starrett 1971) and ongoing surveys of the mussels of Illinois. A third important data base is that on crustaceans, part of which was published (crayfishes and shrimps) by Page (1985). Combined, these data bases can be used to identify outstanding streams by locating those that have the highest diversity (most species) of fishes, crayfishes, and mussels, and those that have the rarest diversity (i.e., those that support populations of threatened and endangered species).

Outstanding streams can also be identified by using the Biological Stream Characterization (BSC), a stream-quality classification developed by the Illinois Department of Conservation and the Illinois Environmental Protection Agency (Hite and Bertrand 1989). The classification is based on fish community characteristics and the potential of a stream to function as a fishery resource. Stream segments are categorized from "A" (highest quality) to "E" (lowest). Currently, 24 stream segments are considered to belong in the "A" category and about 184 in the "B" category.

This year, the Center for Biodiversity at the Illinois Natural History Survey initiated a study to enlarge and enhance the BSC with statewide data on biodiversity. Fieldwork will update existing statewide data bases, specifically those on endangered and threatened species and on the diversity of mussel species. These data, in turn, will be used to identify outstanding streams in addition to those already recognized by the BSC. The end product will be a list of streams to be protected and managed for their outstanding biological characteristics. Although data continue to be gathered, 20 aquatic ecosystems, including 13 streams, were identified as outstanding by Page, Burr, and Cummings (1989) (Table 1), and they seem certain to appear on subsequent lists of streams in Illinois most deserving of protection.

WHAT ARE THE MAJOR CAUSES OF STREAM DEGRADATION?

The recognition of streams worthy of protection is a major accomplishment, but ultimately it becomes a meaningless exercise unless we identify the sources of degradation and initiate actions to eliminate them. Smith (1971) identified factors primarily responsible for the disappearance of some and the decline of other species of fishes in Illinois (Table 2). These factors negatively affect other aquatic species as well and are probably the principal threats to stream biodiversity.

Because of the pervasive nature of agriculture in Illinois, siltation is undoubtedly the major cause of stream degradation and has affected at one time or another nearly every stream in the state. Silt negatively affects stream organisms in several ways and benefits only a few species that are able to tolerate the silt-laden habitats left behind when other species die out. Silt inhibits the ability of organisms to breathe by covering their gills and preventing effective oxygen exchange. High turbidity (silt suspended in water) for prolonged periods results in the suffocation of many aquatic organisms—plants as well as animals. When the primary producers (plants) and primary consumers (e.g., many insect larvae) are eliminated, fishes and other organisms dependent on them for food die or perhaps produce fewer offspring, and eventually species disappear. Silt is unsuitable as a spawning substrate for most fishes because eggs laid in silt are unable to obtain an adequate oxygen supply. Instead, fishes commonly lay their eggs on gravel or among plants, where they are hidden from predators and at the same time remain in actively flowing water and thus in a continuous supply of oxygen. In heavily silted streams where gravel and plants are covered with silt, reproductive success is reduced for many species, and they disappear after a few seasons. Mussels are especially vulnerable because of their sessile habits and, as noted by Cummings (pages 428–438, this volume), the loss of mussel diversity in Illinois has been extraordinarily large (21% of the species have been extirpated and another 35% are in danger of extirpation.)

"Drainage" as a factor contributing to the loss of fishes (Smith 1971) refers to the drainage of bottomland lakes that serve many fishes as nurseries and some stream-dwelling fishes as overwintering refuges and spawning areas. In their natural condition, these lakes are extraordinarily productive (Dodge 1989) and favored areas for the growth and development of small fishes. In Illinois, most of these lakes were found along large rivers such as the Mississippi and Illinois. Their loss resulted from drainage to produce more farmland and from filling with silt as sediment-laden rivers overflowed during periods of flooding. If we are to protect stream organisms, the remaining bottomland lakes must be protected and, where possible, others should be restored.

As more water is consumed in Illinois, primarily for agricultural purposes, water tables

Table 1. Outstanding streams of Illinois based on aquatic biodiversity.

1. Middle Fork Vermilion River, Vermilion County
2. Kankakee River, Kankakee and Will counties
3. Big Creek, Hardin County
4. Embarras River, Jasper, Cumberland, and Coles counties
5. North Fork Vermilion River, Vermilion County
6. Little Vermilion River, Vermilion County
7. Crane Creek, Mason County
8. Lusk Creek, Pope County
9. Kishwaukee River, Winnebago, Boone, and McHenry counties
10. Little Wabash River, Clay, Effingham, and Shelby counties
11. Mississippi River, Rock Island County
12. Wabash River, White County
13. Clear Creek, Union County

Source: Page, Burr, and Cummings 1989.

Table 2. Factors primarily responsible for the extirpation of 8 and decimation of 60 native species of Illinois fishes.

	Number of species extirpated	Number of species decimated
Siltation	2	14
Drainage	0	13
Desiccation during drought	0	12
Species interaction	2	7
Pollution	2	5
Dams and impoundments	0	4
Temperature	0	1
Unknown causes	2	4

Source: Smith 1971.

are lowered in many places and stream desiccation has become a major problem. Springs that were formerly perennial are now ephemeral, and species restricted to them die during periods of drought. The disappearance of the southern redbelly dace, *Phoxinus erythrogaster*, from southern Illinois is thought to be a result of the lower water table and the increased frequency with which springs dry.

Detrimental interactions between exotic and native species include competition, predation, disease, and parasitism. Although some species introduced into Illinois have produced results perceived as beneficial (e.g., certain crops adopted from Europe), the vast majority have proved detrimental to native species. Familiar aquatic examples include the common carp (*Cyprinus carpio*), which is notorious for its ability to stir up stream substrates and destroy otherwise suitable feeding or spawning grounds for other fishes, and the rusty crayfish (*Orconectes rusticus*), which displaces native crayfishes in amazingly short periods of time by means that are not entirely understood. The most recent invader, the zebra mussel (*Dreissena polymorpha*), is now in the Great Lakes and likely to negatively affect native mussels. It is already causing major problems in water treatment and power plants (Cummings 1990).

Much has been written about stream pollution (e.g., Hynes 1960), and it is unnecessary to detail that discussion here. Briefly, pollutants poison aquatic organisms. Major progress has been made recently in reducing point sources of pollution (Illinois Environmental Protection Agency 1990), but such nonpoint sources as the agricultural runoff of pesticides remain a major problem.

Dams and impoundments convert large segments of flowing water into standing water. A few species are favored by the conversion, but many more are eliminated. The pre-impoundment list of species present in a medium to large river in Illinois commonly includes 30–40 species of fishes and 10–20 species of mussels. In contrast, an impoundment typically supports only 8–12 species of fishes and 4–6 species of mussels. The negative impact of an impoundment on biodiversity is compounded by the fact that species in the impoundment are always common, for example, largemouth bass (*Micropterus salmoides*), gizzard shad (*Dorosoma cepedianum*), and common carp (*Cyprinus carpio*); the species lost, however, can include threatened and endangered species. The battle in Illinois over a proposed reservoir on the Middle Fork of the Vermilion River (Figure 3) was in part related to protection of the state-endangered bluebreast darter (*Etheostoma camurum*), and the battle in Tennessee over the proposed Tellico Dam was in part related to the perceived threat to the federally endangered snail darter (*Percina tanasi*). Exacerbating the negative impact of impoundments on biodiversity is their tendency to fill with sediments carried by the streams flowing into them. Because they fill in, they are short-lived relative to the potential life of a stream.

Figure 3. Middle Fork of the Vermilion River, Vermilion County, Illinois. Photo by Lawrence Page.

Dams negatively affect stream communities in addition to the direct effects of inundation. Many species of fishes migrate upstream to spawn; when a dam blocks their passage, they cannot reach suitable spawning areas. In a relatively short time, populations decline and sometimes disappear. A dam impedes and often stops the flow of water downstream and causes major alterations in the stream ecosystem.

In many streams, temperature elevation results in the removal of riparian vegetation that once shaded flowing water. With direct sunlight for prolonged periods, the water is warmed and becomes unsuitable for many species. Another cause of warming is the continuous lowering of the water table, with the result that less groundwater reaches surface streams. Fishes that generally prefer cool water and species adversely affected by this warming trend include trouts, nearly absent from Illinois, and sculpins, which are becoming less common and more restricted in distribution.

Channelization (or canalization) of streams converts them from a series of riffles and pools of varying characteristics into a ditch of nearly uniform width, depth, velocity, and substrate. Instead of providing the variety of habitats available in an unchannelized stream, a channelized stream offers only one habitat and only those species capable of living in that habitat persist. In addition, bankside vegetation is usually removed to enable the large equipment needed for channelization to gain access to the stream. Loss of vegetation further reduces biodiversity. The diversity of species in a ditch is usually much lower than that in a meandering stream.

HOW DO WE PROTECT STREAMS?

Given the major causes of degradation (Table 2) and the multiple uses of streams in Illinois, a multifaceted approach to their protection is imperative. Our goal is to keep the native biota intact, and all approaches aimed at stream protection must have as their objective to keep the stream ecosystem as natural as possible. Broadly considered, protection means that we must prevent the harmful development of the stream and the watershed and the deterioration of the water quality.

A third alternative, restoration (e.g., eliminating the source of a pollutant or allowing a channelized stream to return to a meandering stream) is a reasonable and highly desirable objective and is usually relatively inexpensive. Such massive projects as the restoration of wetlands, although desirable, can be extremely expensive and inevitably fall short of the goal of ecosystem restoration because of the intervening loss of many species previously present. Although a great deal of interest and enthusiasm is being devoted to restoration, if we must choose between protecting the remaining "natural" ecosystems (i.e., those least disturbed by man) and restoring areas, the wiser course is to protect what we have left rather than to devote limited resources to restoring abused ecosystems.

Preventing development. Following the enhancement of the Biological Stream Characterization and the more complete listing of outstanding Illinois streams, I anticipate that the Illinois Nature Preserves Commission, The Nature Conservancy, and other conservation organizations will purchase easements, dedicate preserves, or otherwise move to protect these outstanding aquatic ecosystems. Designation of streams and key portions of watersheds (particularly headwaters) as nature preserves by the Illinois Nature Preserves Commission, the procurement of land by The Nature Conservancy, and similar protective measures would be major steps in keeping stream ecosystems intact because the kinds of development that negatively affect these systems would be prevented.

In addition, when outstanding streams appear on an official list (in this instance, the list generated by the BSC), regulatory agencies can require that development that might negatively affect a stream or its watershed be undertaken in ways that minimize these effects. The identification of healthy and degraded streams will result in a data base that can be extremely useful in other studies on the patterns and causes of stream degradation (e.g., land-use studies).

Protecting water quality. Water quality is protected by preventing the introduction of contaminants such as pesticides and sewage. One extremely important way to reduce the most detrimental nonpoint pollutant, silt, is to keep riparian vegetation intact. In central Illinois, the recent practice of plowing to the stream bank has resulted in stream bank failure and permitted large amounts of silt to enter streams. In addition to its value as a filter of

silt, riparian vegetation shades the stream from direct sunlight during the hottest part of the year, thereby benefiting the many cool-water species characteristic of Illinois streams. Legislation is needed in Illinois to reduce nonpoint pollution.

Other approaches to protecting streams include the development of methods and legislation to restrict introductions of exotic species and to control the amount of water diverted from streams for municipal, industrial, and agricultural uses.

SUMMARY

The present characteristics and biota of the streams of Illinois are the results of geological and evolutionary history and the recent modifications of streams and watersheds by human activities. To protect Illinois streams, we need to determine what aquatic biodiversity remains, where it is located, and what components need to be protected and from what. Then we must develop the most effective means of protection. By supplementing stream quality ratings and statewide data bases on aquatic organisms with fieldwork, we can identify streams with outstanding (i.e., high and rare) biodiversity. After outstanding streams appear on an official state list (the BSC), regulatory agencies can act to minimize environmental damage.

Major threats to the integrity of Illinois streams can be identified and protective measures implemented even though streams, which are affected by activities throughout their watersheds, are clearly more difficult to protect than are many terrestrial ecosystems. Major threats to streams include siltation, drainage of bottomland lakes, desiccation, introductions of exotic species, pollution, artificial impoundments, elevated temperatures, and channelization. Protective measures include the purchase of easements and the dedication of preserves to prevent harmful development of the stream and the watershed. Water quality can be protected by preventing the introduction of detrimental substances such as silt, pesticides, and sewage. One extremely important way to reduce siltation, the most detrimental nonpoint pollutant of streams in Illinois, is to leave riparian vegetation intact. Legislation is needed in Illinois to reduce nonpoint pollution, to restrict introductions of exotic species, and to control the amount of water diverted from streams for municipal, industrial, and agricultural uses.

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Illinois Caves: A Unique Resource

James E. Gardner, Illinois Natural History Survey

Unlike neighboring Missouri with over 5,000 caves, Illinois is not known as a cave state. The many glacial advances that extended far south into the state buried the limestone bedrock that is so conducive to the formation of caves. Nevertheless, according to Oliver and Graham (1988), at least 480 caves are found in Illinois. They noted that the largest and most hydrologically active caves occur in the Sinkhole Plain area of St. Clair and Monroe counties, one of the four major cave areas in Illinois (Figure 1). They also observed that biological activity appears greatest in caves in the Shawnee Hills Section.

The study of caves (speleology) encompasses a unique and intriguing world of darkness, one that often extends far below the earth's surface. Because caves are devoid of sunlight and green plants, they may appear foreboding to any form of life. This perception, combined with the difficult and oftentimes hazardous obstacles for intrepid scientists to overcome, would appear to make speleology an unattractive field of study. To the contrary, speleology is an exciting and rewarding pursuit.

The study of cave life (biospeleology) has not been avoided simply because of potential hazards to investigators. Scientific studies of caves began as early as the 17th century in Europe, when theories on cave hydrology were introduced. Early biospeleology was limited primarily to very general faunal surveys and to descriptions of unpigmented animals (initially thought to be albino) with degenerative eye structures. In the United States, the first cave studies were spearheaded by Europeans. Constantine Rafinesque studied and named cave animals in Mammoth Cave and other caves near Lexington, Kentucky, during his visits around 1822. However, it wasn't until the late 1800s that interest in North American caves and cave life were made fully manifest.

The history of biospeleology in Illinois reaches back over a century when the founder of the Illinois Natural History Survey, Stephen A. Forbes, wrote on blind cave fishes and their allies (Forbes 1881, 1882). The studies that followed much later (Layne and Thompson 1952; Gunning and Lewis 1955; Weise 1957; Smith and Welch 1978) were indirectly associated with caves and springs and focused on the spring cavefish (*Chologaster agassizi*). By 1950, the mass of data that had been collected by nonprofessional biospeleologists, cave explorers, and surveyors encouraged more complete systematic descriptions of taxonomic groups of cave animals and their distribution. Encouraged by a rapidly growing interest in cave ecology and the physiology of cavernicoles (animals found in caves), researchers grew more interested. Peck and Lewis (1977) provided the first and presently only comprehensive information on the occurrence of more than 200 invertebrate species collected from caves in Illinois. The only other studies of invertebrate cave fauna in Illinois focused on taxonomic descriptions (Yeatman 1964; Liang 1970; Steeves and Seidenberg 1971; Lewis and Bowman 1981). Other Illinois studies involving caves (or abandoned mines) did not consider the larger subterranean ecosystem or its inhabitants, but focused on bats that used caves as roosts.

We gained a better understanding of cave ecosystems through studies by Poulson and White (1969), Barr (1968), Caumartin (1963), and Poulson (1972). Perhaps the most comprehensive publication concerning natural cave resources was *The Life of the Cave* by Mohr and Poulson (1966). Biospeleology has now become a recognized field of study. Universities offer degrees with emphasis on aspects of biospeleology, and a number of nonprofit state and national cave research and conservation

organizations actively promote the study and conservation of cave resources. State and federal land management agencies have undertaken studies involving cave resources and the unique life forms associated with them(Gardner 1984, 1986; Oliver and Graham 1988; J.D. Garner, pers. comm.).

There is a great need for more information concerning Illinois caves and their associated fauna. It is my intent to introduce the reader to the rich heritage of our unique cave resources in the hope of fostering appreciation and stimulating continued work. Lipman (1965) commented that "speleology has a definite place on the national conservation scene," and I share his hope that "as the need for more detailed information about underground conditions increases, the science of speleology will grow."

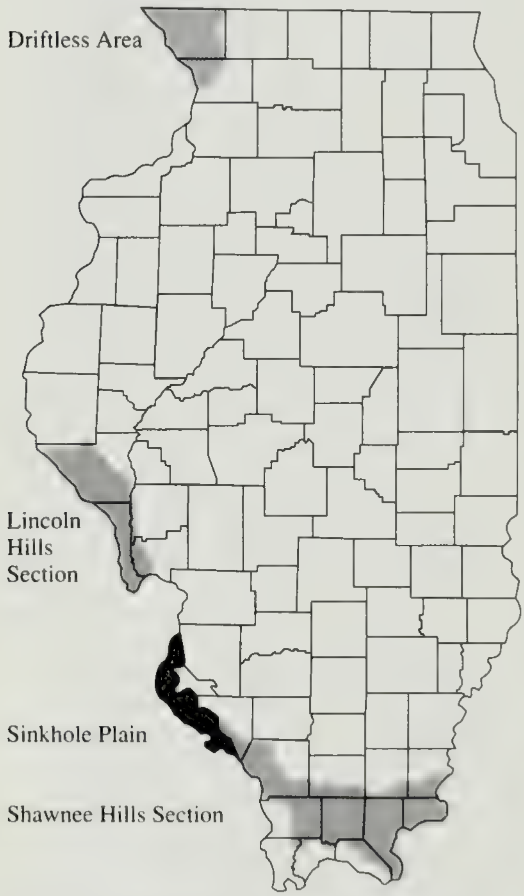

Figure 1. The four major cave areas of Illinois. Adapted from Oliver and Graham 1988.

THE VALUE OF CAVE RESOURCES

Our unique cave habitats and the diversity of life they support are subjected to environmental pressures that threaten their very existence. The delicate balance of many cave ecosystems has been needlessly destroyed by human activities. Caves, springs, and other subterranean features are a valuable part of our natural resources; yet pollution of our subterranean water systems is becoming increasingly evident, damaging the resource and in the process threatening our health and well-being. Cave explorers (spelunkers) must learn to be even more conscientious in order to lessen the impact of their visits. There must be caves left in Illinois free from detrimental impacts, thereby conserving their natural state for future studies.

Caves, like other more traditional natural resources, have four basic values:

Intrinsic. In the most literal sense, caves are a viable and important link in the great environmental chain that binds our planet together. Caves and the resources they contain have an inherent value.

Aesthetic and cultural. Caves provided dwellings for humankind long before recorded history. Often they were sacred places associated with rites and ceremonies. Caves are important historically and aesthetically. Their mystery exists even today and the beauty of untouched cave formations (speleothems) cannot be denied. Caves are a valuable part of our heritage.

Recreational. Spelunking is an increasingly popular recreational sport. As cave locations become known, explorers flock to see them. Anyone who has met the challenge of exploring passageways rarely or never seen will have a memorable and deeply moving experience. Caves have a recreational value but they are also an economic asset, as documented by the millions of tourists who buy tickets yearly for commercial cave tours.

Scientific. Perhaps the most precious value of our caves is found in the knowledge we gain from studying them. Caves, like pages in a history book, provide information on past climate, paleontology, and archaeology.

Caves have perhaps been studied longest by geologists, fascinated by the natural processes of caves (Bretz 1938; Harris and Allen 1952). Hydrologists and engineers have

recognized the need to study caves and the secrets of their formation (speleogenesis). Caves provide a barometer whereby we can measure environmental quality. Dye tracing studies, with their subsequent determination of water courses, have averted serious pollution catastrophes and ensured water quality to many communities. Finally, cave environments and the animals associated with them provide living systems to study. Many cave animals have provided solutions to environmental and medical problems; others serve as examples for the study of basic ecological principles.

BIOSPELEOLOGICAL OBJECTIVES

Howarth (1981) argued that if cave invertebrates were to be targeted for conservation, top priority should be given to conducting thorough biological inventories and ecological studies in threatened caves. He further emphasized that the long-term goal in the conservation of cave invertebrates must be the protection of suitable cave habitats. Poulson (1975) addressed cave management problems and their solutions, noting the importance of baseline biological data. Poulson and Kane (1976) provided an excellent outline for the biological inventory of caves, pointing out that most detrimental impacts could be understood only if a baseline inventory had been conducted before disturbances occurred. The prime objectives of a biological resource inventory according to Poulson and Kane (1976) are summarized below.

Identifying species. As many species of cave animals as possible should be identified and recorded from each cave under investigation. This task is achieved by three methods.

1. A review of the literature. Investigators must be familiar with the work that has preceded their own if they are to conduct inventories efficiently.

2. Identifications in the field. Recorded observations provide a substantial amount of data with minimum impact to the cave environment. Cave invertebrates are among the most difficult life forms to discover, observe, and identify. Specific determinations of invertebrate cave fauna often require a taxonomic specialist. Identifications of vertebrates do not usually require detailed knowledge of microscopic taxonomic characteristics. Bats, salamanders, and certain fishes can be readily identified by trained observers. Collecting and preserving cave vertebrates for the sole purpose of identification is an unacceptable method of inventory. Several species of cave-dwelling vertebrates are protected by state and federal legislation that prohibits their collection.

3. Identification through established collections. Identifications of most cave invertebrates are usually made through reference to existing collections. Specific determinations of fauna are often based on microscopic morphological characteristics (i.e., legs, antennae, mouth parts, reproductive organs). Such identifications are usually well beyond the capabilities of most investigators, and taxonomic specialists need to be consulted.

Documenting cave fauna. Unfortunately, budget constraints significantly limit the extent to which cave resources can be studied. As a result, threatened or endangered species usually receive priorities for study. This limitation should not, however, restrict the gathering of information to only those species. If an ecosystem or habitat approach is followed, all faunal elements in a cave protected for listed species can be studied.

Noting species associations and ecologically related information. The identification of individual elements of a cave's fauna provides insight into the entire ecosystem. Often the occurrence of a particular species can be anticipated by the presence of another species.

Identifying future study areas. Inventories of biological resources are important in identifying caves where more detailed studies are needed. Priorities can then be set since a detailed study of each cave is impossible in terms of time, labor, and money.

Developing recommendations. Cave resources are an integral part of our natural resources, but responsible management or enhancement of any resource cannot be accomplished without first identifying its elements. Cave resources require very special management.

THE CAVE ENVIRONMENT

The cave environment affects the behavior, development, and evolution of the organisms living there. The absence of light, near-constant temperatures, and the amount of humidity all

influence the animals found in caves and their positions within the cave relative to the entrance. Cave climates vary little compared to surface climates. The cave environment is cool and humidity is usually high; evaporation rates, therefore, are very low. Air currents in caves (cave breathing) are normal events in response to surface barometric pressure and can markedly affect temperature and humidity within a cave.

Caves can be divided into zones based on the amount of light and the degree of changes in temperature and humidity.

Twilight zone (cave entrance). The twilight zone extends into the cave as far as unaided human vision is possible. This zone is usually damp and cool, but temperature and humidity fluctuations are close to those found outside the cave. Some green plants may invade the entrance area, and this zone contains the largest and most diverse fauna in the cave. Animals found in the twilight zone include surface species of birds, mammals, snakes, frogs, and many different species of invertebrates that are commonly associated with the surface.

Middle zone. This zone lies just beyond the twilight zone and is characterized by total darkness. Temperature and humidity vary somewhat with seasonal changes at the surface. Animals found in this zone include bats, crickets, millipeds, and surface species of amphipods and isopods.

Zone of total darkness and nearly constant temperature. This zone, like the middle zone, is devoid of light; however, temperatures fluctuate only slightly from the average annual mean temperature of the ground, approximately 13 to 15°C (54 to 58°F) in Illinois. The humidity remains nearly constant, usually near 100%. Animals inhabiting this zone are usually obligative cave-dwelling species such as blind, unpigmented amphipods, isopods, cave fishes, pseudoscorpions, and springtails.

THE CAVE ECOSYSTEM

A cave ecosystem can be defined as all of the living organisms within a given cave bound together by interrelationships and interacting with the physical environment of the cave. Cave animals can be classified by their interaction with the cave environment or by the role they play in the cave ecosystem—their ecological classification (Barr 1963). Some organisms possess highly specialized adaptations that allow them to live in a world of total darkness, extremely low food availability, and relatively constant temperature. The organisms that inhabit caves are divided into two categories: epigean or surface-dwelling organisms and hypogean or subsurface organisms.

Epigean (surface) organisms. These animals usually must complete their entire life cycle on the surface. When found in a cave environment, they are classified as accidentals. Epigeans that wander, fall, or get washed into a cave will either escape or eventually perish there.

Hypogean (subsurface) organisms. These animals normally live below the surface in caves, in subterranean water courses, or in interstitial environments (i.e., between soil particles). The three commonly recognized classes of hypogeans are troglobites, troglophiles, and trogloxenes. The ecological term endogean, or edaphobite, is used to classify species that normally live in soil (e.g., earthworms). Additionally, phreatobite is a term used to describe animals that inhabit the upper layers of groundwater (Holsinger 1969); it is considered synonymous with troglobite. Troglobitic species account for only 20 to 30% of the faunal assemblages of most North American caves. The largest percentages of cave fauna are troglophiles and trogloxenes.

Troglobites, as the derivation of their name suggests (from the Greek for hole and to live), live exclusively in caves, springs, or subterranean water systems; they cannot survive outside these environments. Troglobites are perhaps the most fascinating of all cave species because they possess marked morphological adaptations to subterranean environments. Illinois contains a diversity of troglobitic invertebrates. Peck and Lewis (1977) reported 18 troglobitic invertebrates from Illinois, 14 of which are considered endemic (found nowhere else on earth). However, no populations of troglobitic vertebrates (i.e., true cavefishes and salamanders) are known from the state.

Troglobites possess morphological, physiological, and behavioral adaptations that make them unique. Compared to their surface

relatives, troglobites have reduced metabolic rates. Their sensory capabilities are modified, including reduced or absent vision, increased vibration (hearing) reception, increased olfaction (smell or chemo-reception), and increased tactile sensitivity. Their appendages are longer and more slender, and their movements are slower, more deliberate. Their bodies also tend to be more slender. Reproduction periods are acutely tuned to the seasonal availability of food, and fewer and larger eggs are generally laid.

Troglophiles (cave loving) commonly inhabit caves and can complete their entire life cycle there; however, they are also found in cavelike microclimates on the surface (i.e., deep down in surface leaf debris, in crawl spaces beneath buildings, or inside wet, rotting logs). Examples of troglophiles in Illinois are the cave salamander (*Eurycea lucifuga*) and species of isopods and beetles.

Trogloxenes (cave visitors) frequent caves for shelter and favorable microclimates but must return to the surface to complete some portion of their life cycle (i.e., feeding and reproduction). Bats are classified as trogloxenes as are raccoons, birds that nest in the entrance of caves, and certain species of snakes.

THE NEED FOR CONSERVATION

Bretz and Harris (1961) published descriptions and locations of more than 60 caves throughout Illinois. Their section on basic cave formation (speleogenesis) and cave types is complete and educational. Unfortunately, the publication of the exact locations of these caves opened the way for vandalizing the larger, more popular ones. Enticed by descriptions of passageways and the beautiful formations they contained, novice, adventure-seeking explorers trampled through the caves, defacing and destroying some of the finest cave resources of Illinois.

Relatively few caves have been protected, and many are in dire need of protection. In response to this need, the Illinois legislature passed the Cave Protection Act in 1985. Drafted by the Illinois Department of Conservation (J. D. Garner, pers. comm.), the act established measures for the protection of the natural and cultural resources of Illinois caves. An inventory of the natural resources of over 80 Illinois caves was conducted by the Illinois State Museum (Oliver and Graham 1988). Additionally, the Illinois Department of Conservation and the Illinois Natural History Survey conduct investigations of biological cave resources; emphasis is given to endangered bats.

Recent protection measures for Illinois caves were perhaps precipitated by the recognition (White 1973) and classification (White 1978) of these resources during the Illinois Natural Areas Inventory. As a result of that study and the ongoing efforts of the Illinois Department of Conservation, several caves have been identified as having significant natural resource features and are included in the Illinois Natural Areas Inventory. Other caves have been designated as Illinois Natural Heritage Landmarks in order to protect their valuable resources. One Illinois cave, with at least 12 miles of passageway, was purchased in 1987 and dedicated on August 31, 1989, as an Illinois Nature Preserve to protect a hibernating population of the federally endangered Indiana bat (*Myotis sodalis*). Another cave, Illinois Caverns, was purchased in 1986 and classified as an Illinois Natural Area. Six miles of passageway in Illinois Caverns are open to the public for exploration through a permit system designed to protect the cave.

More studies are needed to identify and understand the unique biological resources of Illinois caves. The delicate and intricate natural communities of our caves cannot be protected unless we identify their elements. However, biological collections in caves should never be done without first consulting competent authorities. Over-collecting and improper collecting methods have been extremely harmful to some populations of cave species. The admonition, "Take only pictures and leave only footprints" should have special significance to every Illinoisan if we are to ensure that our unique cave resource is secured for future generations.

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Session Five: Agro-Urban Ecology

The time has long since passed when a citizen can function responsibly without a broad understanding of the living landscape of which he is a part.—Paul B. Sears

Agricultural and urban development practices that take into account the conservation of the remarkable biodiversity of Illinois must be initiated and encouraged. A balance between economic development and the preservation of natural resources must soon be struck, for it seems that "economics" continues to win and very soon there will be little left to preserve. With the conversion of the landscape to intensive row cropping has come the realization that perhaps our system could operate at a somewhat less intense level. With 99.93% of the landscape of Illinois reflecting some degree of development, the point of no return seems imminent.

Although the production of food is of course beneficial and necessary, the maintenance and restoration of our natural heritage—the landscapes that reflect presettlement conditions complete with the organisms they support—also represents a desirable and perhaps even essential course of action. Common ground must be found between these two opposing courses if the requirements of both are to be met. Perhaps agro-ecology will provide that common ground. In retrospect, we seem to have been moving toward agro-ecology for some time. Consider, for example, the interest shown in organic gardening and low-input and sustainable agriculture. Agro-ecology, however, moves a step closer by requiring a balance between the requirements of agriculture and the obligation to preserve our natural heritage. While our agricultural system presently requires vast biological deserts populated by a single species, the same principles need not be applied to the surrounding landscape. Fields do not have to be cultivated to the very edges of rivers and streams; fencerows and windbreaks do not have to be removed to squeeze in a few more rows of corn; railroad rights-of-way that support corridors of native vegetation do not have to be destroyed; streams do not have to be channelized; and species of organisms need not be driven to extinction in the name of short-term economic development.

The next generation of agriculturalists must farm from an ecological perspective and the time has come when all Illinoisans, farmers and city-dwellers alike, must adopt a conservation ethic. To quote Francis Moore Lappe, "Individual well-being is impossible outside of the well-being of others." Ultimately, we can maintain our well-being only if "others" include all species of organisms, not merely *Homo sapiens*.

Papers read at this session introduced long-range perspectives (for example, the movement of biota between natural and managed ecosystems) as well as more immediate ones (for example, the management of urban deer populations). The closing remarks, both disturbing and challenging, concluded this session and the symposium.

The Land Use Controversy: Maintaining and Increasing Biotic Diversity in the Agricultural Landscape of Illinois

Michael E. Irwin, Illinois Natural History Survey

Approximately one hundred years ago our state underwent a rapid and extensive agricultural transformation that converted the rich, fertile soils and relatively flat terrain underlying its prairies and forests into vast tracts of field crops, primarily corn and soybean. With the exception of Iowa, a state with a history similar to that of Illinois, the Great Plains, with its vast expanses of wheat, and a few large tropical countries like Brazil and Indonesia, which have exploited their lands by putting in broad stretches of such perennial crops as rubber and African oil palm, there is perhaps no extensive area on earth that is so heavily cultivated in so few plant species as the state of Illinois. This agricultural transformation has taken, and continues to take, a heavy toll on native biota. With only 11% of our land now left in natural vegetation and over 53% of our woody plant taxa found in cultivated areas, we have cause for concern. Can this trend be reversed? If so, at what price?

Two viewpoints seem in genuine conflict. On the one hand, we have the argument that agricultural production must be sustained to meet our food needs and to offset the nation's balance of payment deficits through expanded exports. Those holding this short–term view make a powerful case that meeting these needs benefits humanity and our citizens in nutritional and economic ways. On the other hand, the persistent exploitation of our natural areas continues to deplete the biotic richness of our lands, diminishing the legacy for future generations and restricting our access to diverse genes for future manipulation. An equally powerful argument, this long-term perspective recognizes that what is exterminated can never be restored.

I propose that these seemingly opposing positions might be resolved in a manner that satisfies both factions. Aspects of natural systems may enhance agriculture; similarly, aspects of managed landscapes may safeguard natural systems and provide a formula for recovering biotic richness in pillaged habitats.

COMPONENTS FOSTERING SYNERGISM

The components that are responsible for fostering potential synergism must be determined, and the interactions among those components examined. All systems could then be managed with a view towards optimizing selected synergistic interactions. Three elements seem of particular importance: refugia, biological diversity, and genetic richness.

Refugia. Parcels of land that for one reason or another retain unique biota during times when that biota would otherwise not be present are referred to as refugia. How agricultural oases and other biotically favorable, artificial environments sustain species locally through times of natural emigration or diapause and how this ability to sustain biota affects both natural systems and managed landscapes are of considerable consequence.

Irrigation in agricultural settings, particularly in semitropical areas that undergo a season of prolonged drought, can provide habitats favorable for the atypical overseasoning of some biota. As a result, these organisms need not emigrate or aestivate. Irrigation could alter the customary overseasoning habits of a variety of organisms, including insects and their natural enemies, especially in dry tropical forest habitats. Irrigation could also alter the time of year during which certain biota invade natural systems from agricultural settings, with a conceivably enormous impact on both systems. Such invasions already occur regularly in Illinois through the introduction of plants grown in greenhouses for propagation in orchards and home gardens.

Just as agricultural systems provide niches for noncrop-related organisms, so do natural areas harbor both pests and beneficial organisms that either plague or safeguard agricultural crops. The role of refugia in sustaining these complex interactions is relatively unknown; the repercussions, however, are undeniably profound.

Biological diversity. A portion of the diversity of life in one system will inevitably invade nearby systems; how this invasion affects a recipient system is of considerable interest to conservationists and agriculturalists alike. If agriculture is considered an invasive system that receives much of its noncrop biotic diversity in the form of colonists from surrounding systems, the long-term monitoring of colonization might help us to formulate models of invasion rates and types of colonists through time.

Similarly, areas where agroforestry and agriculture are practiced could greatly influence the biological integrity of adjoining natural systems. Scott Robinson (page 382, this volume) provided an example at this symposium when he talked about how habitat fragmentation increased nest parasitism among some of our song birds. Another example is the introduction of the honeybee, which has probably had a great, although unmeasured, impact on natural pollinators in some areas. Monitoring herbivorous insects and their natural enemies might help us develop models of biotic interchange—a third case in point.

Genetic richness. Any biological species consists of a number of populations. Each population includes a number of individuals, each with a slightly different genetic makeup or genotype. The genetic richness within a population purportedly equips that population to withstand environmental disruption, although the process itself is not well understood. When a population from one system invades another, a very restricted portion of the invading population may manage to pass successfully from its resident system and colonize the other. Successful invasions of this nature are sometimes referred to as genetic bottlenecking. The result of colonization and the accompanying extinctions has enormous consequences on the sustainability of a given population, especially one in the area being invaded. The genetic richness of invading populations might well be influenced by the proximity and relative sizes and shapes of the systems in question. Such concepts as habitat fragmentation and patch dynamics are very much a part of this process. Natural systems harbor genetically adaptable populations of harmful and beneficial species that continually invade agricultural systems. Similarly, agricultural landscapes probably contain genetically adaptable populations that continually invade natural systems. Understanding the nature of genetic richness and how that richness affects invasion is important in designing sustainable agricultural and forestry systems.

BIOTIC LINKS

An inevitable exchange of biota occurs wherever two ecosystems come into contact. The zone of interchange, called an ecotone, is in a sense a battleground for genetic and biotic dominance and compatibility. When a natural system is ravaged by deforestation or by the introduction of agriculture, the system usually transforms in stages—for example, from pristine forests to high-input row-crop agriculture. An ecotone is established along the spatiotemporal border of this shift and could well govern the rates and types of biotic interchanges between natural and managed systems. The role of a shifting ecotone in the ecological and economic balance of biota in natural and managed systems remains a mystery and demands investigation.

Refugia, biological diversity, and genetic richness are each affected by successful movement of biota across ecotones. The spatial and temporal links between natural systems and agricultural landscapes can influence the nature and, perhaps more importantly, the rate at which these interactions occur. The size and configuration of areas of land where agroforestry and agriculture are practiced in relation to the size and configuration of the remaining natural area, for instance, could be decisive in determining how managed expanses interact with natural systems.

The movement of biota between natural and managed ecosystems can have dramatic effects on both types of systems. As stewards of this earth, we must manage the effects so

that a balance is achieved between short-term and longer-term goals. The sobering realization is that we know so little about these interchanges and how they affect both types of systems.

Our ability to sustain high-input agriculture has a limited horizon. Time is running out for earth's rich natural ecosystems. We must set a course that will uncover the biotic relationships between these systems so that they can be wisely managed in the future. I urge a strong, timely research and education agenda that critically addresses this issue.

Farm Programs, Agricultural Technologies, and Upland Wildlife Habitat

Richard E. Warner, Illinois Natural History Survey

Since the late 1800s, the grassland habitat of upland wildlife in Illinois has been modified in one way or another by agriculture. Although the prairie was gone by the early 1900s, much of the farmland in Illinois through the 1950s contained various grasses, including small grains, forage crops (cool-season grasses and forage legumes), and uncultivated areas. These farmland mosaics sustained most small vertebrates that had once been common on the prairie, even though pasturing and haying caused significant mortality. After World War II, however, farm programs and agricultural technologies began to change, gradually leading to greater chemical and mechanical disturbances of farmland and the loss of grassland as row-crop farming expanded. By the late 1970s, even the most common upland wildlife—ring-necked pheasant, cottontail, bobwhite, and ground-nesting sparrows—had registered dramatic declines. During the 1980s, the intensive cultivation of corn and soybeans moderated, and grassland was more widely planted, primarily as part of annual set-aside programs that diverted cropland from production. The response of upland wildlife to the reestablishment of grassland has been minimal, presumably because farm programs require or encourage management practices on set-aside fields that are not conducive to the reproduction and survival of most small animals using grassland in Illinois. Moreover, grasslands on farm landscapes now tend to be small, linear patches unattractive to "interior" species. Such highly fragmented tracts also typically sustain high densities of opportunistic mammalian predators. Further, the intensive chemical and tillage disturbances on cropland have limited the availability of insects and plant seeds, the critical food resources of wildlife.

Evaluating Alternatives for Urban Deer Management

James H. Witham, Illinois Natural History Survey

Deer management in metropolitan areas is complicated by the conflicting values of publics with special interests. Those in charge of developing programs that address site-specific needs are well advised to consider various alternatives during the planning stage. Failure to review management options can result in uninformed or biased decisions, which in turn contribute to further controversy and reduce the credibility of those in charge of the program. Published reviews of deer management alternatives generally point out the limitations and advantages associated with various control methods and include an assessment of the usefulness of each method. Relying on such evaluations can be helpful, but making judgments too early, for example at the stage when potential options are being listed, can result in less efficient methods being censored or eliminated prematurely. Early elimination may be detrimental because less efficient methods often have desirable attributes that can be combined with more efficient management techniques. Relying on a combination of methods for the management of deer in urban areas is appealing because it creates a basis for compromise among diverse interest groups.

In large metropolitan areas, such as Chicago, where deer are abundant and adverse interactions with people are widespread and frequent, the state wildlife agency can facilitate local decision making by maintaining a computerized data base of deer management alternatives. Three categories are useful: an unrestricted list of deer management options, potential strategies that rely on a combination of options or suggest how options can be combined, and field-tested management programs and research that document which methods have worked and which have failed and why. Such an information base is one product of the Urban Deer Study conducted by the Illinois Natural History Survey, and we anticipate that it will be used by the Illinois Department of Conservation and the many airports, arboretums, forest preserves, and municipalities in the Chicago Metropolitan Area that manage local deer populations.

Illinois Railbanking Study

Richard Pietruszka, Greenway Coordinator, Illinois Department of Conservation

The Illinois Railbanking Study was initiated by the Illinois Department of Conservation in 1989 in response to the growing recognition within the state and nation that abandoned railroad corridors should be preserved for multiple public uses. Among the objectives of the study are the exploration and evaluation of the natural and outdoor recreational resources associated with the acquisition and development of greenways and their management.

Detailed analyses of the following issues related to the conversion of abandoned railroad corridors into multipurpose public resources were conducted:

> The concerns of local governments and landowners adjacent to abandoned railroad corridors.
>
> The identification and evaluation of strategies that might allay local concerns and resolve conflict.
>
> The evaluation of the economic impact, including the impact on local taxes, of the conversion of abandoned railroad corridors to multipurpose public resources.
>
> The identification of the potential users of converted corridors.

The principle purpose of the Illinois Railbanking Study, concluded in August of 1990, is to assist the Illinois Department of Conservation with the formulation of policies and planning strategies for a statewide trail system.

Closing Remarks

Brian D. Anderson, Director, Illinois Nature Preserves Commission

I was very pleased to be invited to offer the concluding remarks for this symposium. The Illinois Natural History Survey has developed through the years a world-renowned reputation as a center of scientific inquiry. I've found the presentations of the last two days extremely informative, but also disturbing. It is important, I believe, to look at the information provided on various species groups and community types within the context of the landscape on which they occur. Illinois has led the nation in developing institutions like the Natural History Survey, the Endangered Species Protection Board, the Nature Preserves Commission, and the Division of Natural Heritage of the Illinois Department of Conservation—all dedicated to the identification and preservation of the biodiversity of the state. Unfortunately, the founding of these institutions was not by coincidence. No place in the hemisphere has been more drastically altered by the hand of humankind. I might also mention that the statistics I'm about to present were also largely compiled by the Natural History Survey. Over 80% of Illinois is currently committed to agriculture, and another approximately 5% of its surface acreage is urbanized. That leaves approximately 15% of Illinois as undeveloped land. Of that, only 0.07 of 1% retains to some degree its presettlement condition. The full complement of native plants and animals has been forced to survive on less than 100,000 acres of land. The impact to our biota has been devastating; of the approximately 2,500 species of vascular plants considered to be native to Illinois, 356 (about 14%) are considered to be threatened or endangered. Our vertebrate fauna has been even more severely affected: of 649 native vertebrates, 93 (14%) are listed as endangered or threatened, not to mention the 30 or so species that have already been extirpated from our state.

And the carnage continues, but not through spectacular catastrophic events. We can't point to an Exxon Valdez or a Chernobyl. The greatest threat to the native biodiversity of Illinois isn't apocalyptic; it is simply diminution, the slow but steady erosion of our biological heritage—a road here, a 404 permit there, individual by individual, population by population, species by species.

I spent Earth Day in Springfield, and sprinkled among the rally speakers was the reading of a contest-winning essay. The topic was "What Earth Day Means To Me." It caused me to reflect, and I realized I had only hopes for the meaning of Earth Day. And foremost among these was one. I hoped that Earth Day 1990 was the last day I had to listen to the terms *environmental trade-off* and *environmental compromise*. We have to put a word back into our vocabulary—a little word, an important word, the word ***no.*** Where natural areas or habitats of endangered species are involved, we must "just say NO!" If it's a road, take another one. If it's a condo complex, put it somewhere else. If it's an ORV? Well, if it's an ORV, send it back to Japan.

I also listened that day to many speeches heralding our achievements since Earth Day 1970, always with special mention of passage of the Clean Air Act, the Clean Water Act, and the Endangered Species Act. All of these were worthy achievements. They were also all passed in the *first* decade after the *first* Earth Day. And the reauthorization of each was challenged by the Federal Administration in the *second* decade after the first Earth Day Perhaps I am confused, but I thought it was pretty obvious that on Earth Day 1990 we were celebrating the end of a decade of environmental backsliding. It is my hope that Earth Day 1990 was the day that 100 million citizens of the world let the leaders of the western world

know that environmental compromise had no place on any political agenda, conservative or liberal. Planetary survival is, in and of itself, a conservative concept.

A couple of years ago I sat with a conservative acquaintance listening to a presentation on the decline of the natural character of our national parks. He commented that the fellow hadn't learned that the gloom and doom message of radical environmentalism had lost its credibility. The world hadn't ended, and no one wanted to hear that message anymore. I guess he'd missed the news of Love Canal, Three-mile Island, Chernobyl, Bhopal, the donut hole in the ozone layer, and global drought perhaps due to global warming.

Well, I just want to assure him that's not my message. I don't intend to sound morose; however, we have wasted a critical decade. Given our technological sophistication, we should be much farther along in solving our environmental problems, including the biodiversity crisis. So don't worry. We no longer have time for hand wringing. I don't intend to depress you, I intend to *press* you; press you on every front where we possess the technology to improve the environment.

So what is the job before us? First, where the preservation of significant extant resources is involved, we must be uncompromising. We can afford to lose no more. Natural areas, habitats of endangered species, and wetlands are just plain off limits from here on. The developers and planners must hear this message from scientists, conservationists, environmentalists, and politicians. And if the latter are raising their voices in the wrong chorus, they should be sent to look for new jobs.

As for specifics: We must pass legislation to extend the consultation provisions of the Illinois Endangered Species Protection Act to natural areas this session. That legislation was recently introduced as House Bill 3991. (Postscript: it never left committee.)

Second, we must pass strong legislation to protect our remaining wetlands. You can help do that by supporting HB 3712 and SB 1907. (Postscript: neither was brought to the floor of the House of Representatives for a vote.)

Third, we can no longer tolerate the narrow interpretation of the definition of public waters employed by the Division of Water Resources of the Illinois Department of Transportation. Governor Thompson should force the division to accept the Attorney General's opinion, which would extend the division's jurisdiction to most of our streams. If the Division of Water Resources hasn't assumed that responsibility by this time next year, we should have those jurisdictions removed entirely from the Illinois Department of Transportation. (Postscript: a compromise measure was drafted but not introduced.)

Fourth, we should hold every one of our elected representatives responsible for seeing that the first of these three objectives is achieved. (Postscript: *none* was achieved.)

Even if we were to lose nothing else, we probably could not ensure the long-term survival of the biodiversity of our state. We must also *restore* Illinois.

The Illinois Nature Preserves System preserves remnants of high-quality natural communities. Most of these, however, are too small to protect wide-ranging or area-sensitive species. We must begin to establish biotic reserves, which are very large preserves having a high-quality core surrounded by degraded but restorable lands. Using the knowledge we will gain in establishing biotic reserves, we must then, through restoration management, begin to restore our open spaces to native natural communities.

I had a dream a couple months ago. I dreamt I was in a village where everyone, small children to the elderly, were preparing for a wedding. Some were scouring the countryside for rocks and metals; more skilled hands were shaping gemstones and cutting jewels; still others were crafting chains of silver and gold. Finally, the bride appeared; she wasn't a young woman. She was tall—a little wide in the middle—and bore the scars of nurturing several generations of offspring. But when she was draped in that cloak of jewels and gems linked by golden and silver chains, she was transformed into an unparalleled beauty. I see some of those hands in our audience; I've seen them in our nature preserves; I have seen them building conservation areas, restoring railroad prairies, and protecting river corridors. We must do a lot more of all of these things, but we must also integrate our efforts.

I would, therefore, call for the establishment of an Institute of Land Use Studies. The objective of this entity would be to apply the most current computer and satellite technology

available to the identification, protection, preservation, and restoration of our native landscapes—and thereby our biodiversity. This institute would also allow Illinois to lead the nation as *the* center for land use planning technology. The federal government has abdicated its traditional role as a leader in this area. We should, therefore, help ourselves and at the same time develop the tools to preserve other important centers of biodiversity, for example, those in the tropics.

Secondly, we should begin immediately using the Geographic Information System of the Natural History Survey to integrate statewide natural resource planning efforts. Statewide rails-to-trails conversions, watershed planning, nature preserve and biotic reserve establishment, river corridor preservation, wetland protection, and prairie and savanna restoration should all be coordinated through a statewide protection planning committee hosted and chaired by the Department of Energy and Natural Resources.

Thirdly, we should press immediately for sustained funding for natural history survey work. For far too long the Illinois Natural History Survey has been dependent on contracts from private, profit-motivated interests in order to monitor what is happening in Illinois landscapes. For example, although a great effort is underway to complete basic survey work on the state's streams, we are desperate for recent faunistic surveys of habitats of high endemism such as caves, seeps, and springs.

We must also begin to look carefully at invertebrates, including Illinois arthropods. You will notice I didn't even mention the percentage of currently listed invertebrates. Only well-known groups of invertebrates, like mussels and crayfish, have been addressed, and we are not even sure of the total numbers of species in other groups of arthropods. A beetle found in only one cave in Illinois, one cave in the *whole world*, is a treasure; one that I am not prepared to write off.

While we were all pleased that a portion of the real estate transfer tax was dedicated last legislative session to the acquisition of natural areas, there are important natural areas that will not survive the five years required for phasing in the program. We only get 20% of $4 million over the five-year period, 20%, 40%, 60%, 80%, and 100%, respectively. We desperately need a stopgap appropriation or bond issue of about $15 million to acquire such areas before they are lost. Otherwise, as we look forward to achieving the ability to acquire outstanding natural areas, we may have to watch some of our most important natural areas slip between our fingers.

Finally, we must ensure that resources once acquired or protected are adequately managed. I propose that a dollar be added to the license fee for motor vehicles and that the proceeds be dedicated to maintenance and management of natural lands, thereby helping to compensate for the slaughter of wildlife on our highways. Now I've been told everybody and their brother has tried to get a piece of that action, but the very obvious cause-effect relationship between transportation development and loss of wildlife through habitat conversion and habitat fragmentation, not to mention direct wildlife mortality, is so obvious that I believe the public would embrace the surcharge if given the chance.

Thank you for your attention. Thank you for coming, and I look forward to working with all of you in these efforts in the future. Remember, we have an obligation to be objective, to treat all development interests fairly, that is, equally, but we must refrain from compromise. We've already lost too much.

Appendix One: Native Illinois Species and Related Bibliography

Susan L. Post, Illinois Natural History Survey

The assemblage of living forms native to Illinois . . . are held together as a definitely organized, living whole. —Stephen A. Forbes, 1889

The Illinois State Agricultural Society was formed in 1853 and brought zoologists and botanists together in an organized natural history society. In the first transactions of the Agricultural Society, three Illinois species lists were published: *The Birds of Southern Illinois* by H. Pratten (1855), *The Mollusca of Southern Illinois* by H.A. Ulffers (1855), and *The Animals of Cook County* by R. Kennicott (1855). These were the first attempts to list the species of Illinois.

By the turn of the century, biologists from the State Laboratory of Natural History, later to become the Illinois Natural History Survey, were systematically sampling the state. These early field investigations formed the basis for understanding our ecosystems and the natural histories of the organisms found in them. Because of these early records, comparisons can be made between conditions that exist today and those that existed a century ago. From its first publication in 1876, Stephen A. Forbes' *List of Illinois Crustacea*, to its most recent, the Survey has concerned itself not only with cataloging organisms and their distributions in the state but also with the relationships of these organisms to their environments. The Survey's long existence has allowed continuity. Field studies have been and continue to be repeated at intervals, and long-term changes in populations and natural habitats have thereby been documented.

E.O. Wilson (1988) notes in his recent discussion of biological diversity that we do not know the true number of species on Earth, possibly even to the nearest order of magnitude. The same is true for Illinois. We are fairly certain of the numbers of our more visible fauna in the Phylum Cordata—the reptiles, amphibians, fishes, birds, and mammals. In other phyla, however, we are less certain. Research on many of these groups is at an early stage, and new species are frequently found. Even though we list approximately 17,000 insects, this number is only an approximation. The nematodes, which may outnumber even the insects, are an even more difficult group to estimate. The vast majority of the species in Illinois remain unmonitored. Like the dead in Gray's *Elegy Written in a Country Churchyard*, they may pass from the Earth unnoticed and unknown.

The list of species native to Illinois that follows was not generated by a single biological survey but is the result of a search of the literature and a query of systematists familiar with the organisms of Illinois. Sources are listed in the bibliography and in the acknowledgments. The list is divided into five kingdoms: Monera, Protista, Fungi, Plantae, and Animalia (Whittaker 1959). Classification of the invertebrates follows Brusca and Brusca (1990), and plant nomenclature follows Mohlenbrock (1986).

The numbers of certain groups were impossible to estimate and are listed as unknown—the bacteria, nematodes, and protozoa. According to the Bacteriological Code (1958), bacteria cannot be described as simply as other organisms. Every individual is treated as belonging to a number of categories of consecutive rank. Only the individual is considered "real." Until the taxonomic problems have been solved, no list of species for Illinois can be constructed. Although the protozoa are divided into seven phyla (Levine et al. 1980), we have left them as the generic "protozoa." Much of protozoan systematics is still in the alpha stage, with thousands of species yet to be discovered and classified (Lee et al. 1985). Few invertebrate groups illustrate the diversity in form, habitat, and behavior found in the nematodes. An examination of virtually any organic substrate commonly yields nematode specimens representing undescribed species. The systematics of this group is in an embryonic stage.

Although the class Insecta is very large and new species are continually being described, an estimate was made by consulting specialists for each group. The species number for Coleoptera (J. Bouseman, pers. comm.), Hymenoptera (W. LaBerge, pers. comm.), and Diptera (D. Webb, pers. comm.) are only estimates. The number of Diptera was determined by randomly choosing 1,000 species from *A Catalog of the Diptera of America North of Mexico* (Stone et al. 1965) and determining how many of those occur in Illinois. This process was replicated three times and a homogeneity chi square was used to determine if the three samples could be lumped. A nonsignificant x^2 indicated that the three samples could be combined and the mean determined. The percent of species found to occur in Illinois was multiplied by 17,000 (number of species of Diptera in North America) to estimate the number in Illinois.

Only a small fraction of the Illinois fungi are known, but estimates suggested that Illinois has at least 20,000 species (L. Crane, pers. comm.). The number of species of mites in the order Acari was estimated based on the number of mite species in Canada and the assumption that the total number of mites in Illinois would equal half the number of insect species in the state (J. Kethley, pers. comm.). In the class Aves, the number of species includes native breeding species and migrants.

Determining the numbers of species that are extirpated from the state or extinct is difficult. With the exception of the showiest birds, mammals, and flowering plants, biologists are reluctant to say with finality that a species has come to its end. The possibility always exists that a few individuals or a population will be discovered in some remote habitat. As with species numbers, we know with near certainty that some of the more conspicuous fauna have been extirpated; we are less certain about other species.

Species thought to no longer exist in Illinois are listed in Table 1A along with the source from which the determination was made. The plant list was compiled using Sheviak (1978), Paulson and Schwegman (1976), Paulson et al. (1976), and Bowles et al. (1991), and was reviewed by M.L. Bowles, J.E. Ebinger, D.M. Ketzner, G. Kruse, S. Lauzon, L.R. Phillippe, K.R. Robertson, J. Schwegman, M.K. Solecki, and J.B. Taft. The final list was reviewed by K.R. Robertson.

Included in Table 1A are species listed in the 1990 Illinois Endangered Species Protection Board's *Checklist of Endangered and Threatened Animals and Plants of Illinois* but now considered extirpated. Not included are three species of birds, two species of mammals, and one plant species that disappeared from the state and were successfully reintroduced—peregrine falcon, ruffed grouse, wild turkey, white-tailed deer, beaver, and lakeside daisy. Species that no longer occur in the United States are indicated.

The bibliography that concludes this appendix lists all publications that were used to create the list of native Illinois species and the table of extirpated species.

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LIST OF NATIVE ILLINOIS TAXA (AND NUMBERS OF SPECIES)

Kingdom Monera (112+ species)
- Division Schizophyta: bacteria (number of species unknown)
- Division Cyanophyta: blue-green algae (112 species)

Kingdom Protista (1,406+ species)
- Division Protozoa: (number of species unknown)
- Division Euglenophyta: euglenoids (30 species)
- Division Chrysophyta: diatoms and golden brown algae (440 species)
- Division Pyrrophyta: fire algae (20 species)
- Division Chlorophyta: green algae (507 species)
- Division Phaeophyta: brown algae (0 species)
- Division Rhodophyta: red algae (5 species)
- Division Myxomycota: plasmodial slime molds (400 species)
- Division Acrasiomycota: cellular slime molds (2 or 3 species)
- Division Plasmodiophoromycota: (1 species)

Kingdom Fungi (~ 20,000 species)
- Division Chytridiomycota: chytrids (~ 300 species)
- Division Oomycota: water molds (~ 300 species)
- Division Zygomycota: bread molds (~ 400 species)
- Division Ascomycota: sac fungi (~ 9,000 species including 500 species of lichens)
- Division Basidiomycota: club fungi (~ 5,000 species)
- Division Deuteromycota: fungi imperfecti (~ 5,000 species)

Kingdom Plantae (2,574 species)
- Division Bryophyta
  - Class Anthocerota: hornworts (3 species)
  - Class Hepaticae: liverworts (118 species)
  - Class Musci: mosses (385 species including 2 extirpated species)
- Division Lycodiophyta: club mosses, quillworts, and spike mosses (12 species including 3 endangered species of clubmosses and 1 extirpated species of quillwort)
- Division Equisetophyta: horsetails (12 species including 3 endangered and 1 extirpated species)
- Division Filicophyta: ferns (75 species including 11 endangered, 3 threatened, and 2 extirpated species)
- Division Coniferophyta: conifers (14 species, including 4 endangered and 3 threatened species)
- Division Anthophyta: monocots and dicots (1,955 species including 275 endangered, 54 threatened, 53 extirpated, 1 extinct, and 1 extirpated but reintroduced species)

Kingdom Animalia (29,662+ species)
- Phylum Porifera: sponges (14 species)
- Phylum Cnidaria: polyps and jellyfish
  - Class Hydrozoa: hydra and freshwater jellyfish (<10 species of hydra and 1 species of freshwater jellyfish)
- Phylum Platyhelminthes: flatworms (400 species)
- Phylum Nemertea: ribbon worms (1 species)
- Phylum Nematoda: nematodes (number of species unknown)
- Phylum Nematomorpha: horsehair worms (2 species)
- Phylum Acanthocephala: spiny-headed worms (27 species including 1 species found in the endangered greater prairie-chicken)
- Phylum Gastrotricha (60 species)
- Phylum Rotifera: rotifers (150–175 species)
- Phylum Entoprocta (1 species)
- Phylum Annelida: segmented worms
  - Class Oligochaeta: "earthworms" (20 terrestrial and 83 aquatic species)
  - Class Hirudinea: leeches (32 species)
  - Class Aphanoneura (3 species)
  - Class Branchiobdellida: crayfish worms (9 species)

Phylum Arthropoda
- Class Chelicerata (10,598+ species)
  - Subclass Arachnida
    - Order Scorpiones: scorpions (1 species)
    - Order Araneae: spiders (530 species)
    - Order Pseudoscorpionida: pseudoscorpions (28 species)
    - Order Opiliones: daddy long-legs (19 species)
    - Order Acari: mites and ticks (20 species of ticks and ~10,000 species of mites)
- Class Myriapoda (74 species)
  - Subclass Diplopoda: millipedes (29 species)
  - Subclass Pauropoda: pauropods (5 species)
  - Subclass Chilopoda: centipedes (37 species)
  - Subclass Symphyla: symphylans (3 species)
- Class Insecta (~17,000 species)
  - Subclass Myrientomata
    - Order Proturans: proturans (6 species)
  - Subclass Oligoentomata
    - Order Collembola: springtails (73 species)
  - Subclass Diplurata
    - Order Diplura: diplurans (6–10 species)
  - Subclass Zygoentomata
    - Order Thysanura: silverfish (6+ species)
  - Subclass Pterygota
    - Order Ephemeroptera: mayflies (126 species)
    - Order Odonata: dragonflies (98 species) and damselflies (44 species)
    - Order Blattodea: cockroaches (9 species)
    - Order Mantodea: mantids (1 species)
    - Order Isoptera: termites (5 species)
    - Order Plecoptera: stoneflies (57 species)
    - Order Orthoptera: grasshoppers, crickets, and katydids (157 species)
    - Order Dermaptera: earwigs (3 species)
    - Order Phasmida: walking sticks (5 species)
    - Order Zoraptera: zorapterans (1 species)
    - Order Psocoptera: book and bark lice (91 species)
    - Order Hemiptera: true bugs (910 species)
    - Order Thysanoptera: thrips (200 species)
    - Order Anoplura: sucking lice (18 native and 19 nonnative [from domestic animals and man] species)
    - Order Mallophaga: biting lice (280 species including 1 extinct species that occurred on the passenger pigeon)
    - Order Homoptera: plant bugs (1,485 species)
    - Order Strepsiptera: twisted-wing insects (15–20 species)
    - Order Coleoptera: beetles (5,000 species)
    - Order Neuroptera: lacewings, antlions, alderflies (45 species including 1 extirpated species)
    - Order Hymenoptera: bees, ants, wasps (2,000+ species)
    - Order Mecoptera: scorpionflies (18 species)
    - Order Siphonaptera: fleas (33 species including 1 species that occurs on the endangered Eastern wood rat)
    - Order Diptera: true flies, mosquitoes, and gnats (4,100 species)
    - Order Trichoptera: caddisflies (184 species)
    - Order Lepidoptera: butterflies and moths (2,000 species including 1 endangered, 2 threatened, and 5 extirpated species)
- Subphylum Crustacea
  - Class Branchiopoda (52 species)
    - Order Anostraca: fairy shrimp (4 species)
    - Order Cladocera: water fleas (~43 species)
    - Order Conchostraca: clam shrimp (5 species)
  - Class Maxillopoda (84 species)
    - Subclass Ostracoda: seed shrimp (53 species)
    - Subclass Copepoda (21 species)
    - Subclass Branchiura: fish lice (10 species)

Class Malacostraca (71 species)
Order Decapoda: crayfish (23 species including 4 endangered and 2 extirpated species)
Order Isopoda: pillbugs (28 species including 1 endangered species)
Order Amphipoda: scuds (19 species including 5 endangered and 1 threatened species)
Order Musida: opossum shrimp (1 species)
Phylum Pentastomida: tongue worms (no species found in native fauna)
Phylum Tardigrada: water bears (13 species)
Phylum Mollusca
Class Gastropoda: snails (170 species including 1 endangered species)
Class Bivalvia: mussels and clams (104 species including 29 endangered, 4 threatened, 16 extirpated, and 4 extinct species)
Phylum Ectoprocta (9 species)
Phylum Chordata
Subphylum Vertebrata
Class Agnatha: lampreys and jawless fish (6 species including 1 endangered and 1 threatened species)
Class Osteichthyes: boney fishes (181 species including 12 endangered, 14 threatened, and 12 extirpated species)
Class Amphibia: amphibians (39 species including 2 endangered, 1 threatened, and 1 presumed extirpated species)
Class Reptilia: reptiles (59 species including 5 endangered, 4 threatened, and 1 presumed extirpated species)
Class Aves: birds (297 native breeding and migrant species including 37 endangered, 6 threatened, 8 extirpated, 4 extinct, and 3 extirpated but reintroduced species)
Class Mammalia: mammals (67 species including 7 endangered, 3 threatened, 9 extirpated, and 2 extirpated but reintroduced species)

Total number of species: 53,754+
Total number of extirpated species: 115
Total number of threatened and endangered species: 497

Table 1A. Native Illinois species presumed extirpated.

Scientific name	Common name	Source
KINGDOM PLANTAE		
Division Bryophyta		
Brachylema subulatum (P. Beauvois) Schimper ex Cardot	Moss	McKnight pers. comm.
Neckera pennata Hedwig	Moss	McKnight pers. comm.
Division Lycodiophyta		
Isoetes engelmannii A. Braun	Englemann's quillwort	Mohlenbrock 1967
Division Equisetophyta		
Equisetum palustre L.	Marsh horsetail	Bowles et al. 1991
Division Filicophyta		
Asplenium ruta-muraria L.	Wall-rue spleenwort	Mohlenbrock 1967
Woodwardia virginica (L.) J.E. Smith	Chain fern	Bowles et al. 1991
Division Anthophyta		
Apios priceana Robinson	Price's groundnut	Schwegman pers. comm.
Arabis drummondii Gray	Rock cress	Swink & Wilhelm 1979
Arethusa bulbosa L.	Dragon's mouth	Sheviak 1974
Bacopa acuminata (Walter) B.L. Robinson	Purple hedge-hyssop	Bowles et al. 1991
Baptisia tinctoria (L.) R. Brown	Yellow wild indigo	Bowles et al. 1991
Carex cumulata (Bailey) Fernald	Sedge	Bowles et al. 1991
Carex plantaginea Lamarck	Sedge	Bowles et al. 1991
Cinna latifolia (Treviranus) Grisebach	Drooping wood reed	Bowles et al. 1991
Cirsium pitcheri (Torrey & Eaton) Torrey & Gray	Dune thistle	Bowles pers. comm.
Clintonia borealis (Aiton) Rafinesque	Bluebead lily	Swink 1988
Corallorhiza trifida Chatelain	Pale coral root orchid	Sheviak 1974
Daucus pusillus Michaux	Small wild carrot	Bowles et al. 1991

Scientific name	Common name	Source
Delphinium carolinianum Walter var. *penardii* (Huth) Warnock	Prairie larkspur	Mohlenbrock 1981
Elatine brachysperma Gray	Waterwort	Mohlenbrock 1978
Eleocharis caribaea (Rottboell) Blake	Spike rush	Mohlenbrock 1976
Eleocharis equisetoides (Elliott) Torrey	Horsetail spike rush	Bowles et al. 1991
Epigaea repens L. var. *glabrifolia* Fernald	Trailing arbutus	Swink & Wilhelm 1979
Erianthus brevibarbis Michaux	Brown plume grass	Mohlenbrock 1973
Fuirena scirpoides Michaux	Umbrella grass	Bowles et al. 1991
Gaillardia aestivalis (Walter) Rock	Blanket flower	Mohlenbrock 1986
Geum rivale L.	Purple avens	Bowles et al. 199
Glyceria canadensis (Michaux) Trinius	Rattlesnake manna grass	Bowles et al. 1991
Gnaphalium macounii Greene	Western cudweed	Bowles et al. 1991
Gratiola aurea Muhlenberg	Goldenpert	Swink & Wilhelm 1979
Hippuris vulgaris L.	Mare's tail	Swink & Wilhelm 1979
Hypericum ellipticum Hooker	St. John's wort	Mohlenbrock 1978
Linnaea borealis L. ssp. *americana* (Forbes) Hulten	Twinflower	Swink & Wilhelm 1979
Malaxis monophylla (L.) Swartz	Adder's mouth orchid	Sheviak 1978
Malaxis unifolia Michaux	Adder's mouth orchid	Sheviak 1978
Nemopanthus mucronata (L.) Trelease	Mountain holly	Mohlenbrock 1978
Oryzopsis asperifolia Michaux	Rice grass	Mohlenbrock 1972
Oryzopsis pungens (Torrey) Hitchcock	Rice grass	Mohlenbrock 1972
Paspalum lentiferum Lamarck	Bead grass	Bowles et al. 1991
Plantago heterophylla Nuttall	Small plantain	Bowles et al. 1991
Platanthera (Habenaria) dilatata (Pursh) Hooker	White orchis	Sheviak 1974
Platanthera (Habenaria) hookeri Torrey	Hooker's orchid	Bowles et al. 1991
Platanthera (Habenaria) orbiculata (Pursh) Torrey	Round-leaved orchid	Sheviak 1974
Polygala paucifolia Willdenow	Flowering wintergreen	Swink & Wilhelm 1979
Potamogeton epihydrus Rafinesque	Pondweed	Mohlenbrock 1970a
Potamogeton vaseyi J.W. Robbins	Pondweed	Bowles et al. 1991
Ranunculus ambigens S. Watson	Spearwort	Bowles et al. 1991
Ranunculus gmelinii DC. var. *hookeri* (D. Don) L. Benson	Small yellow crowfoot	Swink & Wilhelm 1979
Schedonnardus paniculatus (Nuttall) Trelease	Tumble grass	Mohlenbrock 1972
Scheuchzeria palustris L. var. *americana* Fernald	Arrow grass	Bowles et al. 1991
Scirpus microcarpus Presl	Bulrush	Bowles et al. 1991
Scirpus pedicellatus Fernald	Bulrush	Bowles et al. 1991
Scirpus subterminalis Torrey	Bulrush	Swink & Wilhelm 1979
Sparganium minimum (Hartman) Fries	Least bur-reed	Mohlenbrock 1970a
Thismia americana N.E. Pfeiffer[1]	Thismia	Mohlenbrock 1983
Trautvetteria caroliniensis (Walter) Vail	False bugbane	Mohlenbrock 1981
Trifolium stoloniferum Eaton	Running buffalo grass	Schwegman 1989
Trillium cernuum L.	Nodding trillium	Bowles et al. 1991
Valerianella patellaria (Sullivant) Wood	Corn salad	Sheviak 1978
KINGDOM ANIMALIA		
Phylum Arthropoda		
Class Insecta		
Columbicola extinctus Malcomson	Chewing louse on passenger pigeon	Malcomson 1937
Hesperia dacotae (Skinner)	Dakota skipper	Sternburg pers. comm.
Notodonta simplaria Graef	Simple promenant	Godfrey pers. comm.
Pieris napi oleracea (Harris)	Mustard white	Irwin & Downy 1973
Schinia indiana (J.B. Smith)	Indiana schinia	Godfrey pers. comm.
Speyeria diana (Cramer)	Diana fritillary	Irwin & Downy 1973
Sympherobius occidentalis Fitch	Brown lacewing	Macleod pers. comm.
Class Malacostraca		
Cambarus robustus Girard	Lusty crayfish	Page 1985
Macrobrachium ohione (Smith)	Ohio shrimp	Page 1985

Scientific name	Common name	Source
Phylum Mollusca		
Class Bivalvia		
Epioblasma flexuosa (Rafinesque)[1]	Leafshell	Cummings 1991
Epioblasma obliquata (Rafinesque)	Catspaw	Cummings 1991
Epioblasma personata (Say)[1]	Round combshell	Cummings 1991
Epioblasma propinqua (Lea)[1]	Tennessee riffleshell	Cummings 1991
Epioblasma rangiana (Lea)	Northern riffleshell	Cummings 1991
Epioblasma sampsonii (Lea)[1]	Wabash riffleshell	Cummings 1991
Epioblasma torulosa (Rafinesque)	Tubercled blossom	Cummings 1991
Fusconaia subrotunda (Lea)	Long-solid	Cummings 1991
Hemistena lata (Rafinesque)	Cracking pearlymussel	Cummings 1991
Lampsilis abrupta (Say)	Pink mucket	Cummings 1991
Leptodea leptodon (Rafinesque)	Scaleshell	Cummings 1991
Obovaria retusa (Lamarck)	Ring pink	Cummings 1991
Plethobasus cicatricosus (Say)	White wartyback	Cummings 1991
Pleurobema plenum (Lea)	Rough pigtoe	Cummings 1991
Quadrula fragosa (Conrad)	Winged mapleleaf	Cummings 1991
Villosa fabalis (Lea)	Rayed bean	Cummings 1991
Phylum Cordata		
Class Osteichthyes		
Atractosteus spatula (Lacépède)	Alligator gar	Burr 1991
Coregonus nigripinnis (Gill)	Blackfin cisco	Smith 1979
Crystallaria asprella (Jordan)	Crystal darter	Smith 1979
Esox masquinongy Mitchill	Muskellunge	Smith 1979
Etheostoma histrio Jordan & Gilbert	Harlequin darter	Burr 1991
Hybopsis amblops (Rafinesque)	Bigeye chub	Burr 1991
Ichthyomyzon bdellium (Jordan)	Ohio lamprey	Smith 1979
Lythrurus ardens (Cope)	Rosefin shiner	Smith 1979
Noturus stigmosus Taylor	Northern madtom	Burr 1991
Percina evides (Jordan & Copeland)	Gilt darter	Smith 1979
Percina uranidea (Jordan & Gilbert)	Stargazing darter	Smith 1979
Pteronotropis hubbsi (Bailey & Robison)	Bluehead shiner	Burr 1991
Class Amphibia		
Cryptobranchus alleganiensis (Daudin)	Hellbender	Morris pers. comm.
Class Reptilia		
Nerodia fasciata (Linnaeus)	Broad-banded watersnake	Morris pers. comm.
Class Aves		
Ajaia ajaja (Linnaeus)	Roseate spoonbill	Bohlen 1989
Campephilus principalis (Linnaeus)[1]	Ivory-billed woodpecker	Bohlen 1989
Conuropsis carolinensis (Linnaeus)[1]	Carolina parakeet	Bohlen 1989
Corvus corax Linnaeus	Common raven	Bohlen 1989
Cygnus buccinator Richardson	Trumpeter swan	Bohlen 1989
Ectopistes migratorius (Linnaeus)[1]	Passenger pigeon	Bohlen 1989
Numenius borealis (Forster)[1]	Eskimo curlew	Bohlen 1989
Tympanuchus phasianellus (Linnaeus)	Sharp-tailed grouse	Bohlen 1989
Class Mammalia		
Bison bison (Linnaeus)	Bison	Hoffmeister 1989
Canis lupus Linnaeus	Gray wolf	Hoffmeister 1989
Cervus elaphus Linnaeus	Elk	Hoffmeister 1989
Erethizon dorsatum (Linnaeus)	Porcupine	Hoffmeister 1989
Felis concolor Linnaeus	Mountain lion	Hoffmeister 1989
Martes americana (Turton)	Marten	Hoffmeister 1989
Martes pennanti (Erxleben)	Fisher	Hoffmeister 1989
Peromyscus gossypinus (Le Conte)	Cotton mouse	Hoffmeister 1989
Ursus americanus Pallas	Black bear	Hoffmeister 1989

[1] This species no longer occurs in the United States.

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Appendix Two

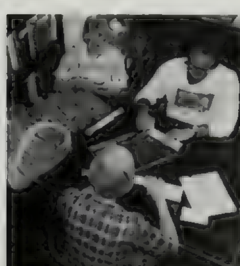
County reference map. Readers who wish to identify counties on maps shown in the text will find this map a convenient reference.

Coffee break allowed time for speaker Joyce Hofmann to continue her advocacy on behalf of those troubled wetland tenants, the swamp rabbit and rice rat.

Brooks Burr's concern over threatened fish and dwindling aquatic habitat answered Thoreau's query, "Who hears the fishes when they cry?" We do.

Louis Iverson's use of satellite data piqued interest in INHS Special Publication 11: *Forest Resources of Illinois* with its 67 computer-generated maps.

James "Gene" Gardner's research on caves introduced us to the fragility and fascination of that dark and silent habitat.



Survey support staff set up exhibits for the symposium and rolled posters for mailing. In an economy drive, staff collected the 450 paper towel tubes used to mail the posters!

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Sabine M. Huhndorf

Illinois Natural History Survey Bulletin
Volume 34, Article 5
May 1992

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A Division of the Illinois Department of Energy and Natural Resources

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Introduction

The genus *Leptosphaeria* was established by Cesati and de Notaris (1863) to include 26 species. The original description was superficial by modern standards and relied primarily on ascospore characteristics to delimit the genus. Cesati and de Notaris described ascospores as oblong or fusoid, two- to many-celled, and hyaline becoming yellow to dark brown. Because other structural features were poorly defined, a wide range of ascomycetes has been included in this genus. The 1,689 taxa described in *Leptosphaeria* (Crane and Shearer 1991) represent, according to current concepts of ascomycete classification, a mixture of Hymenoascomycetes and Loculoascomycetes. Crane and Shearer (1991) and Müller (1950) provide good reviews of the historical background of the genus *Leptosphaeria*. Holm (1957) and Shoemaker (1984a) consider a limited number of species.

A large number of intergeneric transfers of *Leptosphaeria* species have been made in the past 50 years. Five genera—*Phaeosphaeria* Miyake, *Paraphaeosphaeria* Eriksson, *Nodulosphaeria* Riess, *Entodesmium* Riess, and *Ophiobolus* Riess—have become accepted repositories for many *Leptosphaeria* species (Holm 1957; Leuchtmann 1984; Shoemaker 1976, 1984a,b). *Paraphaeosphaeria*, *Nodulosphaeria*, and *Entodesmium* are well defined by several morphological features, including ascocarp wall structure and ascospore characteristics (Shoemaker 1984b, Shoemaker and Babcock 1985). *Phaeosphaeria* is separated from *Leptosphaeria* by several morphological characters and host specialization but has itself become a very large and diverse genus (Shoemaker and Babcock 1989b). *Ophiobolus* species intergrade with long-spored species of *Leptosphaeria* (Shoemaker 1976). For a key to genera variously allied with *Leptosphaeria*, see Shoemaker (1984a) or Leuchtmann (1984).

Holm (1957) considered 62 species of *Leptosphaeria* and restricted the genus to those species most similar to the type of the genus, *Leptosphaeria doliolum* (Pers.:Fr.) Ces. & de Not. He emphasized the anatomy of the ascocarp wall and found that in most *Leptosphaeria* species the wall consisted of thick-walled cells termed scleroplectenchyma. He also emphasized the identity of the substrate and the structure of the ascocarp relative to the substrate in relegating a number of *Leptosphaeria* species to other genera. Excluded species were distributed in *Nodulosphaeria*, *Phaeosphaeria*, and *Entodesmium*. He gave considerable weight to the family of host plants in distinguishing these genera. Holm's (1957) scheme was accepted by Shoemaker (1984a) in his treatment of Canadian species of *Leptosphaeria*.

In recent years, *Leptosphaeria* has been included in various orders in the Bitunicatae or the Loculoascomycetes. Luttrell (1973) placed *Leptosphaeria* in the family Pleosporaceae of the Pleosporales. The single order Dothideales was used by von Arx and Müller (1975) for all fungi classified as Loculoascomycetes; they retained *Leptosphaeria* in the Pleosporaceae. Eriksson and Hawksworth (1986) classified the genus in the family Phaeosphaeriaceae of the Dothideales. Barr (1987a) placed *Leptosphaeria* in the family Leptosphaeriaceae of the Pleosporales. Most recently, Eriksson and Hawksworth (1990) accepted the family Leptosphaeriaceae in the order Dothideales. Barr's classification of the Ascomycota (1983, 1987a) is employed in this dissertation because of its relationship to previous classification schemes (Luttrell 1973) and its detailed explanation of the relationship of taxa. Barr's orders and families are based upon combinations of developmental and morphological characteristics that reflect the widespread diversity within the group. Barr's classification provides a key to higher taxa and is practical

for identification and for determining the placement of organisms not yet included in the scheme.

The present research reassesses the taxonomic position of species of *Leptosphaeria* described from plants in the family Rosaceae. In doing so, this work emphasizes a concept of *Leptosphaeria* based on its type species. Because discrete groups of morphologically similar species were found on related hosts (*Nodulosphaeria* on Compositae, *Phaeosphaeria* on Gramineae and *Entodesmium* on Leguminosae), a goal of the study was to determine whether a distinct group of related species could be found on Rosaceous hosts. Also, approaching the taxonomy of this large, complex genus on the basis of host family is a convenient way of dividing the large numbers of *Leptosphaeria* species into smaller, workable groups.

Fifty-five species described from Rosaceous hosts have been included in *Leptosphaeria* (see appendix). Efforts were made to locate and obtain type material for all of the described species. The names of herbaria providing material are abbreviated in this dissertation according to Index Herbariorum (Holmgren et al. 1990). When possible, type specimens were studied, supplemented by other collections, and the species were redescribed and illustrated from the type material. Unfortunately, type material could not be located for all of the species; in such cases, descriptions were based on other material only when the resulting concept of the species was obviously in accordance with the original description. From this work, it became apparent that no discrete group of related species is specialized on the Rosaceae. The species studied were determined to represent a mixture of Loculoascomycetes and Hymenoascomycetes, and non-*Leptosphaeria* species were reassigned to more appropriate genera.

Materials and Methods

Several techniques were employed to assess character states of specimens. Fungi were observed microscopically in water mounts for details of asci, ascospores, hamathecium, centrum, and ascocarp wall surface, using bright-field and Nomarski differential interference contrast. India ink was used as a negative stain to reveal ascospore sheaths. Melzer's reagent (0.5 g iodine, 1.5 g KI, 20.0 g chloral hydrate, 20.0 ml distilled water) was used to observe amyloid reactions in unitunicate asci. Semipermanent mounts were made in lactophenol, and many of the photomicrographs were made from these mounts. Micrographs were made using Kodak T Max 100 and Kodak Technical Pan film 2415 (Eastman Kodak Company, Rochester, New York). For scanning electron microscopy, dry ascocarps and substrate were used direct from the herbarium specimen, without any preparation. Specimens were viewed with an Amray 1830 scanning electron microscope.

The order of septation in ascospores is given following Shoemaker (1984a). The sequence of septation is recorded chronologically, with 1 being the first septum formed. A series of numbers separated by colons indicates the sequence in which the septa form. The first number represents the septum nearest the ascospore apex, and the last number is the septum nearest the base. Unusual or infrequent occurrences are recorded within parentheses (Shoemaker 1984a).

To observe details of ascocarp anatomy, semi-thin sections of the ascocarp were needed for light microscopy. Fixation and embedding techniques for plastic were developed to obtain good, uniform sections from dried fungal material in a relatively short period of time. The techniques for fixation and embedding are given in Huhndorf (1991).

Discussion of Characters

Semi-thin sections of ascocarps were used to assess characteristics of the ascocarp walls. Wall characteristics have proved useful in taxonomic placement of species but may have limitations in the routine identification of specimens. It may be possible to observe this feature with hand sections or frozen microtome sections, as done by Shoemaker (1984a). Ascocarp walls of cells radiating in surface view (textura prismatica) and thick-walled cells (scleroplectenchyma) are good indicators within *Leptosphaeria* of alliance with *L. doliolum*. Wall cells in surface view are seen easily from crush mounts. Semi-thin sections and scanning electron microscopy give a good indication of the relationship of the ascocarp to the substrate. This character has also proved

important in delimiting *Leptosphaeria*; included species have ascocarps that are superficial or that become superficial. Semi-thin sections also show ostiole structure, a characteristic that is important in related genera such as *Nodulosphaeria*.

Ascospore characters, in combination with other characters, are useful for placement of species. *Leptosphaeria* species have more or less fusiform, three- to multi-septate ascospores with some pigmentation. These character states are continuous rather than discrete, and in practice, divisions are made in a somewhat arbitrary manner. Also, ascospore pigmentation varies within a species and may reflect age, environmental influences, and/or substrate. Ascospore wall ornamentation often is difficult to assess, especially when using type material, which frequently is old and in poor condition. In addition, type material is usually of uniform developmental stage and frequently is sparse and depleted by the activities of previous researchers. Ascospore wall ornamentation is difficult to assess with the light microscope because of the limits of resolution, except in cases for which there may be unusually distinctive surface ornamentation. Using the scanning electron microscope to resolve surface features requires sufficient material of an appropriate developmental stage, with the ascospores released from the asci and with surface detail not obscured by sheaths or mucilaginous material. Unfortunately, this situation does not usually exist in type material. In recent collections with different developmental stages it is easier to view ascospore wall ornamentation. Although the taxonomic significance of this character is unclear at this time, largely because of the difficulties involved in studying it, further studies would be useful.

The importance of host specificity or substrate preference in delimiting species or genera needs further clarification. Whether substrate preference does occur and can be used as a taxonomic character can be demonstrated only by extensive collection and comparison of species from a variety of substrates, by comparative study of the morphology of pure cultures of species obtained from a variety of substrates and grown under identical environmental conditions, and by determining experimentally the range of substrates on which isolates of species will grow and reproduce.

The structure of the interascal filaments, part of what Eriksson (1981) termed the hamathecium, plays an important role in distinguishing members of the Melanommatales from those in the Pleosporales according to Barr's (1987a) classification. Only one member of the Melanommatales was found in this group of species, and the diagnostically important trabeculate pseudoparaphyses were difficult to recognize. It was placed in that group because of a combination of other characters. The distinction between cellular pseudoparaphyses (filaments that appear septate at 450x magnification and branch and anastomose) and trabeculate pseudoparaphyses (thin filaments that do not appear septate at 450x magnification and branch and anastomose) seems to be clear only in certain cases; the pseudoparaphyses often appear as continuous, rather than discrete, character states. Trabeculate pseudoparaphyses can be mistaken for cellular ones if septa appear regularly and anastomoses are sparse.

Ascus morphology, emphasized by Eriksson (1981), was not employed in this study because of the difficulty in observing modes of ascus dehiscence and details of ascus wall layers in type and other herbarium specimens. Also, in most cases, the use of stains to enhance ascus wall layers gave virtually no results.

Leptosphaeria Species Referable to the Pleosporales

All of the species in this chapter belong in the Pleosporales (*sensu* Barr 1987a) and share a combination of character states, any one of which may deviate somewhat for a particular taxon. These characters include cellular pseudoparaphyses, asci in a basal layer, a peridium that is usually pseudoparenchymatous, and bipolarly asymmetrical ascospores. The families included within the order are the Leptosphaeriaceae, Phaeosphaeriaceae, and Lophiostomataceae.

Leptosphaeriaceae

The Leptosphaeriaceae as defined by Barr (1987a) include five genera united by the characters of coelomycetous anamorphs, asci that are narrower and thinner-walled than in the Pleosporaceae, and ascocarp walls that consist of relatively large, thick-walled or scleroplectenchymatous cells. The only genus in the family treated here is *Leptosphaeria*.

Leptosphaeria V. Cesati & G. de Notaris, Commentario della Societa Crittogamologica Italiana, Milan 1:234. 1863. Nomen conservandum.

Lectotype: *Sphaeria doliolum* C.H. Persoon: E.M. Fries.

Ascocarps scattered or clustered, superficial or immersed beneath epidermis, becoming superficial as epidermis is shed, conic globose, subglobose or depressed, glabrous, papillate. **Ascocarp wall** often of radiating textura prismatica in surface view; in longitudinal section usually more than three cells thick, composed of scleroplectenchyma, often with an external crust. **Papilla** central, short, sometimes longer and beaklike, without hyaline periphyses. **Pseudoparaphyses** broad or narrow, septate, anastomosing, with or without guttules, septal thickenings, and gelatinous coating. **Asci** bitunicate, numerous in a broad basal hymenium, cylindrical to clavate, short-stalked, 8-spored in most, with spores often biseriate or overlapping uniseriate. **Ascospores** fusiform, clavate, 3 or more septate, primary septum often median and often constricted, some shade of yellow or brown, appendages or sheath may or may not be present. **Anamorphs** coelomycetous where known (see Crane and Shearer 1991).

The concept of *Leptosphaeria* accepted here is essentially that of Holm (1957), later adopted by Shoemaker (1984a) with some modification. The lectotypification of *L. doliolum* (Shearer et al. 1990) represents a basis for circumscribing the genus. More emphasis is placed on scleroplectenchyma found in the ascocarp walls than is considered important by Shoemaker (1984a). As Shoemaker (1984a) noted, thin sections are essential to show this thick-walled cell structure in which the lumen of the cells is very small. Emphasis is also placed on the wall tissue arrangements in surface view, described using the textura types of Korf (1958). Species having a tissue arrangement similar to that of *L. doliolum*, of cells radiating in surface view (textura prismatica), are regarded as most typical, but species without this character state are not necessarily excluded. The position of the ascocarp relative to the substrate is very important, with included species having either superficial ascocarps or ascocarps immersed beneath the epidermis and becoming superficial as the epidermis is shed. Because only type or herbarium specimens were studied, anamorphs were not considered because cultures could not be made from this dead material.

Examination of 28 purported species of *Leptosphaeria* from the Rosaceae revealed five species that fit the adopted generic concept. The excluded species are treated following these five species.

Key to species of *Leptosphaeria* on the Rosaceae

1a. Ascocarp wall cells radiate 2
1b. Ascocarp wall cells randomly oriented 4
  2a. Ascocarp superficial or immersed becoming superficial, ascospores mature inside centrum 3
  2b. Ascocarp immersed beneath host cuticle, ascospores mostly maturing on substrate surface .... *L. umbrosa*
    3a. Neck papillate, short conic, ascospores narrowly fusiform, 22–28 x 4–5 µm .... *L. doliolum*
    3b. Neck cylindrical, beaklike, ascospores broadly fusiform, 17–20 x 5–8 µm .... *L. praetermissa*
4a. Ascocarp immersed-subepidermal, wall pseudoparenchyma, or partly scleroplectenchyma, on leaves of *Cercocarpus* (provisionally retained within *Leptosphaeria*) .... *L. cercocarpi*
4b. Ascocarp erumpent to superficial, wall scleroplectenchyma, on *Dryas* .... *L. dryadophila*

•*Leptosphaeria doliolum* (C.H. Persoon:E.M. Fries) V. Cesati & G. de Notaris, Commentario della Societa Crittogamologica Italiana, Milan 1:234–235. 1863. See Figure 1.

≡ *Sphaeria doliolum* C.H. Persoon:E.M. Fries, Icones et Descriptiones Fungorum Minus Cognitorum, p. 39. 1800; E.M. Fries, Systema Mycologicum Sistens Fungorum 2:509. 1823.

= *Leptosphaeria rustica* P.A. Karsten, Fungi Fenniae Exsiccati, Century 10, No. 964. Anno 1870.

≡ *Metasphaeria rustica* (P.A. Karsten) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:157. 1883.

Ascocarps scattered, sparse, immersed-subcuticular to erumpent, papillate, glabrous to tomentose at base, globose, flattened at base, 300–325 µm diameter, 250–300 µm high. **Ascocarp wall** of textura prismatica in surface view, composed of cells radiating from apex outward; in longitudinal section 45–55 µm thick at sides, 20–27 µm thick at base, composed of 12–15 layers of hyaline, polygonal, isodiametric, scleroplectenchymatic cells (3.6–6.5 µm diameter), outer 2–3 layers somewhat brown-melanized, with an external brown-melanized crust. **Papilla** broadly rounded, not fully formed, 130–135 µm high, 70–75 µm wide; wall 40–50 µm thick, composed of 15–20 layers of small, brown-melanized, thick-walled, polygonal, isodiametric cells (2.5–6.5 µm diameter), outer layers heavily brown-melanized, inner layers hyaline, surrounding a 20–25 µm wide immature circular ostiole formed from small hyaline cells, without periphyses. **Pseudoparaphyses** 1.0–2.0 µm wide, 150–175 µm long (height of the ascocarp cavity), numerous, narrowly cellular, with guttule-like thickenings at septa, without gelatinous coating. **Asci** 90–125 x 5–9 µm, numerous, basal, cylindrical-clavate, with 8 overlapping uniseriate ascospores. **Ascospores** 22–28 x 4–5 µm, narrowly fusiform, with acute end cell shape, second cell slightly enlarged, straight to slightly curved, 3-septate, septa evenly distributed, order of septation 2:1:2, primary septum median and slightly constricted; light brown, guttulate, without appendages, surrounded by gelatinous material.

Lectotype: As *Sphaeria doliolum* Pers., 910.270-650 (L).

Exsiccatae: Finland: Tammela, on *Spireae ulmaria* L. (=*Filipendula ulmaria* Maxim.), Sept., Fungi Fenniae Exsiccati, Century 10, No. 964 (isotype of *L. rustica*, H, FH).

Comments: The collections of *L. rustica*, on stems of *Spiraea ulmaria* L. in both of the exsiccatae sets, were immature. No ascospores were found, and asci were only beginning to form. Karsten (1873) describes the ascospores as elongate-fusoid, subhyaline, uniseptate with several guttules in each cell, and 30–36 x 5–6 µm in size. He probably described immature spores. This information—along with the

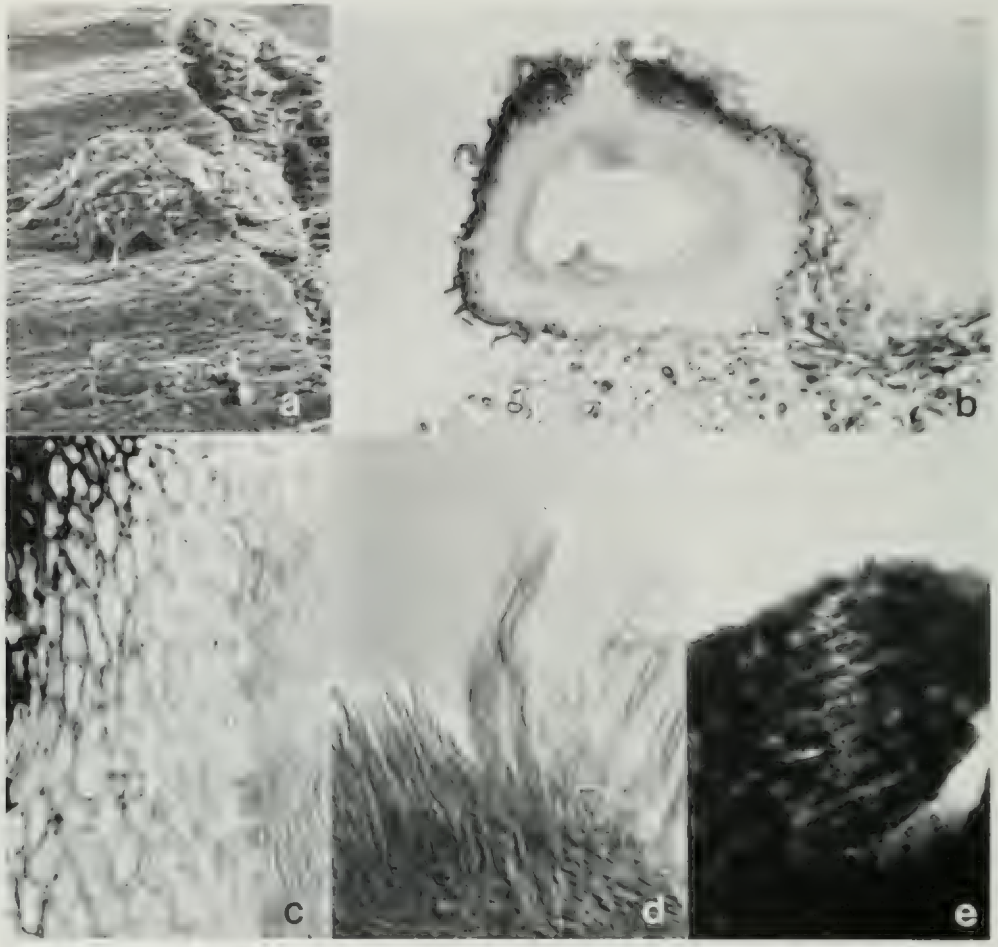

Figure 1. *Leptosphaeria doliolum.* a. SEM of erumpent ascocarp, x125. b. longitudinal median section through ascocarp, x150. c. longitudinal, median section through ascocarp wall, x950. d. ascus, x525. e. ascocarp wall surface with radiating cells, x550. All from isotype of *L. rustica.*

radiating wall cells in surface view, the scleroplectenchymatic wall cells in section, and the location of the ascocarp relative to the substrate—is consistent with the character of *L. doliolum*, the type of the genus. *Leptosphaeria doliolum* is found on many dead herbaceous stems, although not previously described from *Spiraea.*

•*Leptosphaeria dryadophila* S.M. Huhndorf nom. nov. See Figure 2.
Etymology: Gr. philos = having affinity for.
≡ *Melanomma dryadis* C.J. Johanson in Rabenhorst, Fungi europaei no. 3659 (1890). (Basionym).
= *Leptosphaeria dryadis* E. Rostrup, Botanisk Tidsskrift 25:305. 1903.

Ascocarps clustered, erumpent to superficial, papillate, glabrous to slightly tomentose toward base, tomentum of dark brown hyphae, conic-globose, 150–250 μm diameter, 180–275 μm high. **Ascocarp wall** of textura angularis in surface view; in longitudinal section uniformly 12–20 μm thick (up to 27 μm thick near apex), composed of 4–5 layers of polygonal, isodiametric to slightly elongate, scleroplectenchymatic cells, outer 2–3 layers composed of brown-melanized cells (3.5–4.3 x 5.5–6.8 μm), inner 2–3 layers composed of hyaline, compressed cells (2.1–3.5 x 10.0–12.3 μm). **Papilla** conical, 60–65 μm high, 25–50 μm wide at the apex, 90–110 μm wide at the base, composed of 7–9 layers of isodiametric cells (2.8–3.6 μm diameter), wall 10–12 μm thick surrounding a 35–45 μm wide ostiole without

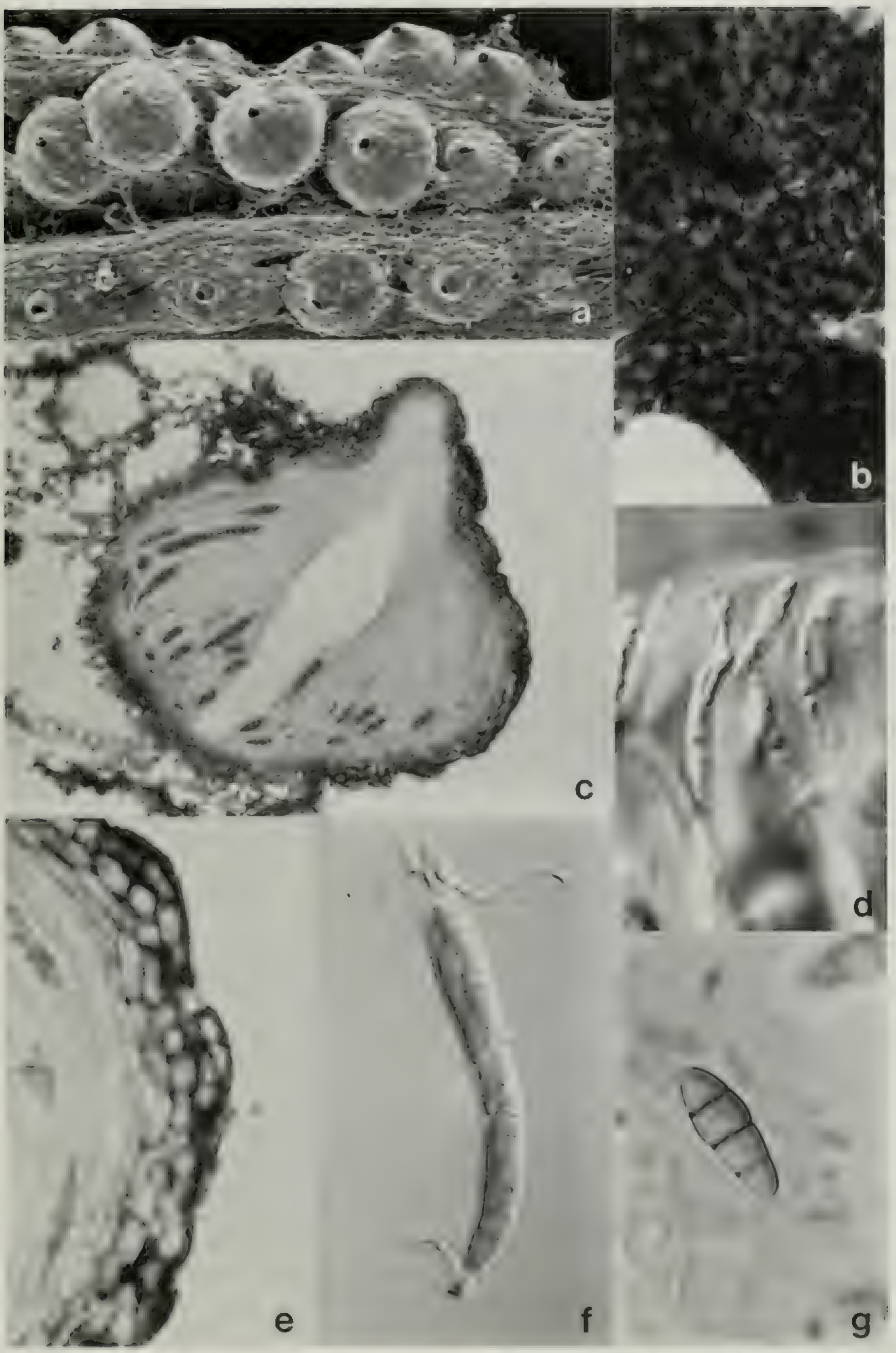

Figure 2. *Leptosphaeria dryadophila*. a. SEM of erumpent ascocarps, x50. b. ascocarp wall surface, x550. c. longitudinal median section through ascocarp, x250. d. cellular pseudoparaphyses, x2,000. e. longitudinal median section through ascocarp wall, x950. f. ascus, x500. g. ascospore, x1,150. a, c, e, and f from holotype of *L. dryadis*; b, d, and g from isotype of *L. dryadophila*.

. eriphyses. **Pseudoparaphyses** 0.7–3.0 µm wide, 110–175 µm long (height of the ascocarp cavity), numerous, narrowly cellular, with gelatinous coating. **Asci** (72–)90–118 x 10.8–13.6 µm, numerous, basal to slightly lateral, cylindrical, thin-walled but with a thickened rounded apex, short-stalked, with 8 biseriate ascospores. **Ascospores** 20.1–24.5 x 5.7–7.2 µm, fusiform to slightly clavate, with acute end-cell shape, slightly curved; 3(-4-5)-septate, septa evenly distributed, order of septation 2:1:2(:3:4), without constrictions; pale brownish yellow, with ornamented wall, without sheath or appendages.

Isotype: SWEDEN: Jamtland, Renfjallet, c. 900m, in fructibus et calycibus emortuis *Dryadis octopetalae* L. 13, Juli 1884, leg. C.J. Johanson, Rabenhorst, Fungi europaei no. 3659 (1890) (FH, NY).

Exsiccatae: SWEDEN: Jamtland, Renfjallet, 13, Juli 1884, leg. C.J. Johanson, Vgr., Micr. rar. sel. 105 (FH).

Other material examined: ICELAND: Sponsgerdi, on *Dryas octopetala*, Juli 12, 1901, O. Davidson (type of *Leptosphaeria dryadis*, C).

Comments: This fungus was originally described in *Melanomma* and was retained with some reservation in that genus by Holm (1957, 1979), who stated, "The species is hardly a *Melanomma* but its true affinities are doubtful to me." *Melanomma dryadis* differs from the current concept of *Melanomma* (Barr 1987a) in not having asci that arise peripherally within the centrum and not having trabeculate pseudoparaphyses. Barr (1982) erected the genus *Bricookea* for a biologically similar species, *Bricookea sepalorum* (Vleugal) Barr, which is found on the inflorescences of *Juncus* species. *Melanomma dryadis* differs from this fungus in several respects: cells of the ascocarp wall are scleroplectenchymatous, not pseudoparenchymatous; the ascocarp apex opens by a pore, not by a slit; and the ascospores are not hyaline. *Melanomma dryadis*, occurring in and on the dead flowers and fruits of *Dryas octopetala*, is a true *Leptosphaeria*, having the characteristics of an erumpent to superficial ascocarp with a wall of scleroplectenchymatous cells and 3-septate yellow-brown ascospores. It does not, however, show the radiating arrangement of cells of the ascocarp surface characteristic of *L. doliolum*. Because the epithet *dryadis* is pre-empted in *Leptosphaeria* by *L. dryadis* Rostrup, a new name, *Leptosphaeria dryadophila* is proposed for *Melanomma dryadis* Johanson.

•*Leptosphaeria praetermissa* (P.A. Karsten) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:26. 1883. See Figure 3.

≡ *Sphaeria praetermissa* P.A. Karsten, Fungi Fenniae Exsiccati, Century 9, No. 852. Anno 1869.

Ascocarps clustered, sparse, immersed-subepidermal becoming erumpent, papillate, glabrous to tomentose at base, globose, flattened at base, 350–625 µm diameter, 300–500 µm high. **Ascocarp wall** of textura prismatica in surface view, composed of cells radiating from apex outward; in longitudinal section uniformly 32–58 µm thick at sides and base, composed of 7–8 layers of hyaline, polygonal, isodiametric, scleroplectenchymatic cells (5.7–13.6 x 3.6–7.2 µm), inner 2–3 layers somewhat elongate and compressed, with an external brown-melanized crust. **Papilla** beaklike, cylindrical, erumpent, 120–180 µm high, 75–135 µm wide; wall 25–36 µm thick, composed of 5–6 layers of small, brown-melanized, thick-walled, polygonal, isodiametric cells (4.3–7.2 µm diameter), surrounding a 35–80 µm wide circular ostiole formed from small hyaline cells, without periphyses. **Pseudoparaphyses** 1.0–2.0 µm wide, 180–260 µm long (height of the ascocarp cavity), numerous, narrowly cellular, without gelatinous coating. **Asci** 100–130(–150) x 7–13 µm, numerous, basal, cylindrical, thin-walled, short-stalked, rounded apex with apical chamber present, with 8 biseriate ascospores. **Ascospores** 17–20(–25) x 5.5–8.0 µm, broadly fusiform, end cells acute to rounded, straight to slightly curved; 3-septate, septa evenly distributed, order of septation 2:1:3 or 2:1:2, primary septum median, with constrictions at all septa, second cell occasionally enlarged (wider); brownish-yellow, smooth, without sheath or appendages.

Isotype: FINLAND: In caulibus emortuis *Rubi odorati* et *R. idaei* in par. Tammela sat fre-

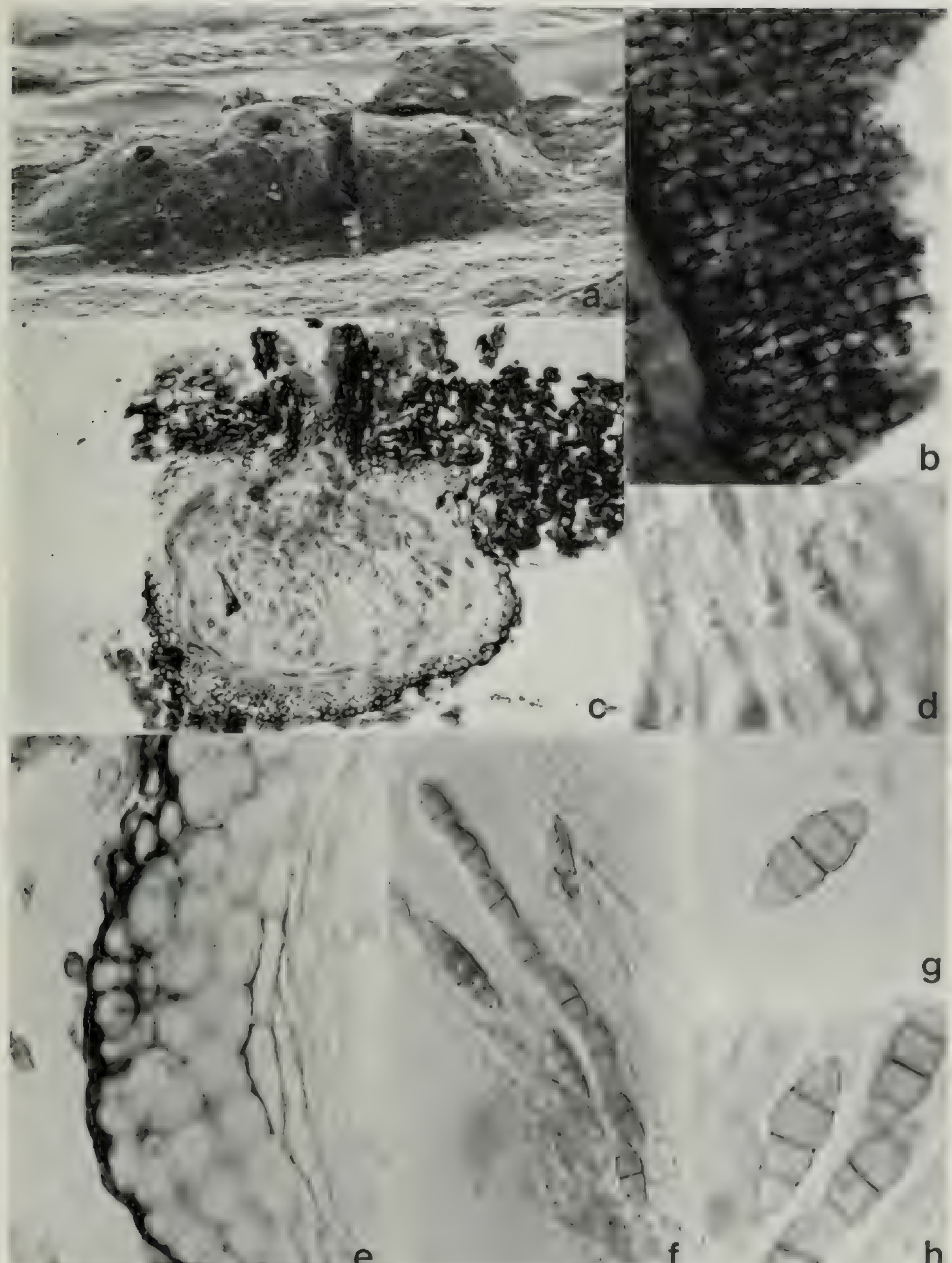

Figure 3. *Leptosphaeria praetermissa*. a. SEM of erumpent ascocarps, x65. b. ascocarp wall surface with radiating cells, x550. c. longitudinal median section through ascocarp, x150. d. cellular pseudoparaphyses, x2,000. e. longitudinal median section through ascocarp wall, x950. f. ascus, x525. g, h. ascospores, x1,150. All from isotype of *L. praetermissa*.

quenter per annum obvia. Fungi Fenniae Exsiccati, Century 9, No. 852 (H, FH).

Other material examined: CANADA: Quebec: Gatineau Provincial Park, Chemin Ridge Road, on *Rubus odoratus*, 20 Jun. 1987, C.T. Rogerson (NY); SWEDEN: Jemtland: Five collections, all on *Rubus ideaus*, Leg. A.G. Eliasson, 20 May 1930, 27 Jun. 1930, 17 Jun. 1931, 19 Jun. 1931, 28 Jul. 1931 (S); Umea, Apr. 1908, J. Vleugel (S).

Comments: *Leptosphaeria praetermissa* warrants inclusion in the genus because of its large erumpent ascocarp with a wall composed of scleroplectenchymatous cells. As in *L. doliolum*, the wall has an external crust, and the cells form a radiating pattern in surface view. It differs from *L. doliolum* in having a rather long, cylindrical neck that grows through the host epidermis before the ascocarp becomes erumpent. This species seems to be found predominantly in Europe but is probably not common there. It was not encountered in any collections of *Rubus* sp. in the United States but was found in one collection from Canada.

•*Leptosphaeria umbrosa* G. Niessl *in* G.L. Rabenhorst, Fungi Europaei Exsiccati, Klotschii Herbarii vivi Mycologici Continuatio, Edition 3 (Edita Nova), Series 2, Century 20, No. 1934. Anno 1875; Just's Botanisch Jahresberichte 3:262. 1887. See Figure 4.

≡ *Massaria umbrosa* (G. Niessl) H. Rehm *in* P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 9:761. 1891.

Ascocarps scattered, immersed-subcuticular, papillate, glabrous, globose, flattened at base, 150–300 µm diameter, 90–200 µm high. **Ascocarp wall** of textura prismatica in surface view, composed of cells radiating from apex outward; in longitudinal section 4–6 µm thick at the base, composed of thin, hyaline, compressed cells, 10.8–22 µm thick at the sides, composed of 5–6 layers of polygonal, scleroplectenchymatic cells, outer 2–3 layers of isodiametric to slightly elongate, brown-melanized cells (3.5 x 7–10 µm) surrounded by a brown-melanized crust, inner 2–3 layers of hyaline, elongate-compressed cells (2–3 x 10–18 µm). **Papilla** bluntly conical, (18–)25–54 µm high, 36–56 µm wide at the apex, 60–70 µm wide at the base, composed of 5–6 layers of small, isodiametric, heavily brown-melanized, thick-walled cells (2–3.6 µm diameter), wall 14.4–22 µm thick surrounding a 25–45 µm wide ostiole without periphyses. **Pseudoparaphyses** 0.7–2.0 µm wide, 80–110 µm long (height of the ascocarp cavity), numerous, narrowly cellular, with guttule-like thickenings at septa, without gelatinous coating. **Asci** (72–) 80–100(–117) x 10.8–15.0 µm, numerous, basal, cylindrical-clavate, thick-walled, rounded apex with apical chamber, short-stalked, with 8 tri- to biseriate ascospores, most commonly immature. **Ascospores** 27.3–33.0 x 4.3–7.2 µm, hyaline to subhyaline when immature, 28–37.4 x 5.7–9.3 µm, pale brown when mature, narrowly fusiform, with acute end-cell shape, slightly curved; 4-septate, septa unevenly distributed, order of septation 2:1:2:3, primary septum supramedian and slightly constricted, second cell slightly enlarged at maturity, slightly roughened wall, continuous sheath (0.7–1.5 µm thick) surrounding immature spore, without appendages.

Holotype: AUSTRIA: An *Spiraea Aruncus* [=*Aruncus dioicus* (Walt.) Fern.] bei Voitsberg in Steiermark. Septbr. 1874 (M).

Exsiccatae: AUSTRIA: Voitsberg, Steiermark, Septbr., G. v. Niessl, Rabenhorst, F. europaei exs. 1934 (FH, NY isotypes); Voitsberg, Steiermark, Aug. 1882, G. v. Niessl, Rehm, Ascomyceten 690 (FH, NY authentic material); Voitsberg, Steiermark, G. v. Niessl, Weese, Eumycetes sel. exs. 638 (FH).

Other material examined: GERMANY: Frauenfeld, on Solidago, October (NY).

Comments: *Leptosphaeria umbrosa* is interesting because initially it seems to resemble members of the Phaeosphaeriaceae having small, pseudoparenchymatic-walled, subcuticular ascocarps that lift the host cuticle on maturity. Upon closer examination, it reveals the characteristic features of *Leptosphaeria* such as ascocarp walls composed of scleroplectenchyma surrounded by an external brown crust and wall cells that radiate in surface view. Other distinctive characteristics that may aid in the identification of this species are the wide pseudoparaphyses with prominant thickenings at the septa and mature

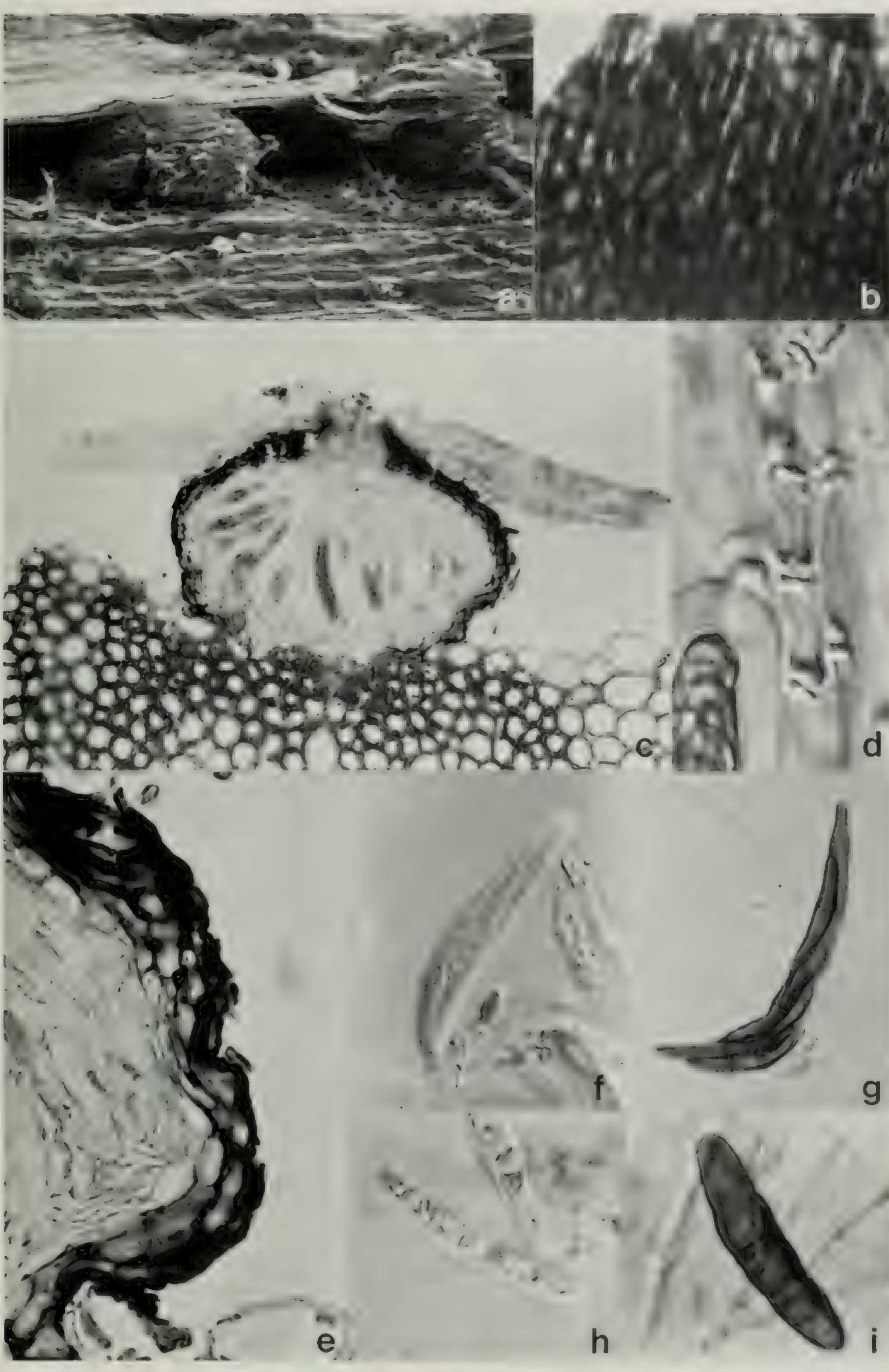

Figure 4. *Leptosphaeria umbrosa*. a. SEM of immersed ascocarps, x150. b. ascocarp wall surface with radiating cells, x550. c. longitudinal median section through ascocarp, x200. d. cellular pseudoparaphyses with thickenings at septa, x2,000. e. longitudinal median section through ascocarp wall, x950. f. ascus with immature ascospores, x525. g. ascus with mature ascospores, x525. h. immature ascospore, x1,150. i. mature ascospore from substrate surface, x1,150. All from holotype of *L. umbrosa*.

brown ascospores that are often seen only on the surface of the substrate surrounding the ascocarp. Also diagnostic are the thin ascocarp bases often left behind on the substrate when ascocarps are removed from the substrate surface.

•*Leptosphaeria cercocarpi* H. Sydow & P. Sydow, Annales Mycologici 5:339. 1907. See Figure 5.

Ascocarps clustered, abundant, immersed-subepidermal, with surrounding stroma extending into substrate, papillate, glabrous, globose, 175–240 µm diameter, 175–240 µm high. **Ascocarp wall** of textura angularis-globulosa in surface view; in longitudinal section 22–31 µm thick at sides and base, up to 50 µm thick near apex, composed of 6–8 layers of polygonal, isodiametric-elongate, pseudoparenchymatic cells [3.6–7.2 x 5.4–12.6(–16) µm], outer 2–4 layers of brown-melanized cells at sides and base, inner 4–5 layers of hyaline-compressed cells at base. **Papilla** very short, erumpent, rounded-conical, 31–45 µm high, 62–93 µm wide, wall 25–30 µm thick, composed of 8–10 layers of small, isodiametric, scleroplectenchymatic cells (2.0–7.2 µm diameter), outer 5–6 layers brown-melanized, inner 3–4 layers hyaline, surrounding a 30–40 µm wide circular ostiole without periphyses. **Pseudoparaphyses** 1.0–2.0 µm wide, 125–200 µm long (height of the ascocarp cavity), numerous, narrowly cellular, with gelatinous coating. **Asci** 95–120 x 17–21 µm, numerous, basal, cylindrical-oblong, thick-walled, short-stalked, rounded apex, with 8 biseriate ascospores. **Ascospores** (25–)27–31(–33) x 8.5–11.5 µm, broadly fusiform to slightly clavate, end cells rounded, straight to slightly curved, 3-septate, septa evenly distributed, order of septation 2:1:2, primary septum median, slight constrictions at all septa, brown, ornamented walls, without sheath or appendages.

Holotype: United States: In foliis emortuis *Cercocarpi ledifolii*, Mill Creek Canyon, Salt Lake Co., Utah Americae bor. leg. A.O. Garrett no. 677 (S).

Other material examined: United States: Utah: Box Elder Co., One Mile Creek, north side of Raft River Mts., Aug. 25, 1986; Juab Co., 5.2 mi up Granite Creek Canyon, east side of Deep Creek Mts, Aug. 26, 1986; Rich Co., Sunrise Campground, Cache National Forest, Route 89, west of Garden City, July 13, 1985; Weber Co., Malans Peak, Aug. 11, 1972; Weber Co., south slope of Malans Peak, Wasatch Mts., east of Ogden, July 1, 1976; Weber Co., mouth of Taylor's Canyon, Wasatch Mts., east of Ogden, May 18, 1972, Apr. 29, 1981, May 6, 1982, all on *Cercocarpus ledifolius* Torrey in Torrey & Gray var. *intermontanus* (Brittonia 39:424. 1987), all C.T. Rogerson (all NY).

Comments: *Leptosphaeria cercocarpi* is an easily recognized species on *Cercocarpus ledifolius*. The ascocarps usually entirely cover both surfaces of dead leaves. Retaining this species in *Leptosphaeria* is not totally satisfactory, but placing it elsewhere is also problematic. Certain characteristics resemble those found in the Phaeosphaeriaceae (*sensu* Barr 1987a). The ascocarps are small-medium sized and immersed in the substrate, and there appears to be some kind of hyphal growth or stroma surrounding the ascocarps and extending into the substrate. Other characteristics do not coincide with inclusion in that group. Although the lateral walls of the ascocarp of *L. cercocarpi* consist of pseudoparenchymatous cells, they are not thin and soft as is characteristic of the Phaeosphaeriaceae. In fact, the walls in the upper regions of the ascocarp consist of thick-walled scleroplectenchymatous cells. In Barr's (1987a) key to this family, the only two genera in which this fungus could be placed are *Phaeosphaeria* and *Kalmusia*. The ascocarps are not small and delicate enough for inclusion within *Phaeosphaeria*, and the current concept includes only species on monocots (Shoemaker and Babcock 1989b) (but see also the discussions for *P. pomona* and *P. lucilla* herein). The current concept of *Kalmusia*, which includes *K. clivensis* (see discussion herein), does not adequately accommodate *L. cercocarpi*. Therefore, unlike other leaf-inhabiting species of *Leptosphaeria* belonging elsewhere (i.e., Phaeosphaeriaceae), this species is retained within *Leptosphaeria* because of the larger, robust nature of the ascocarp and wall.

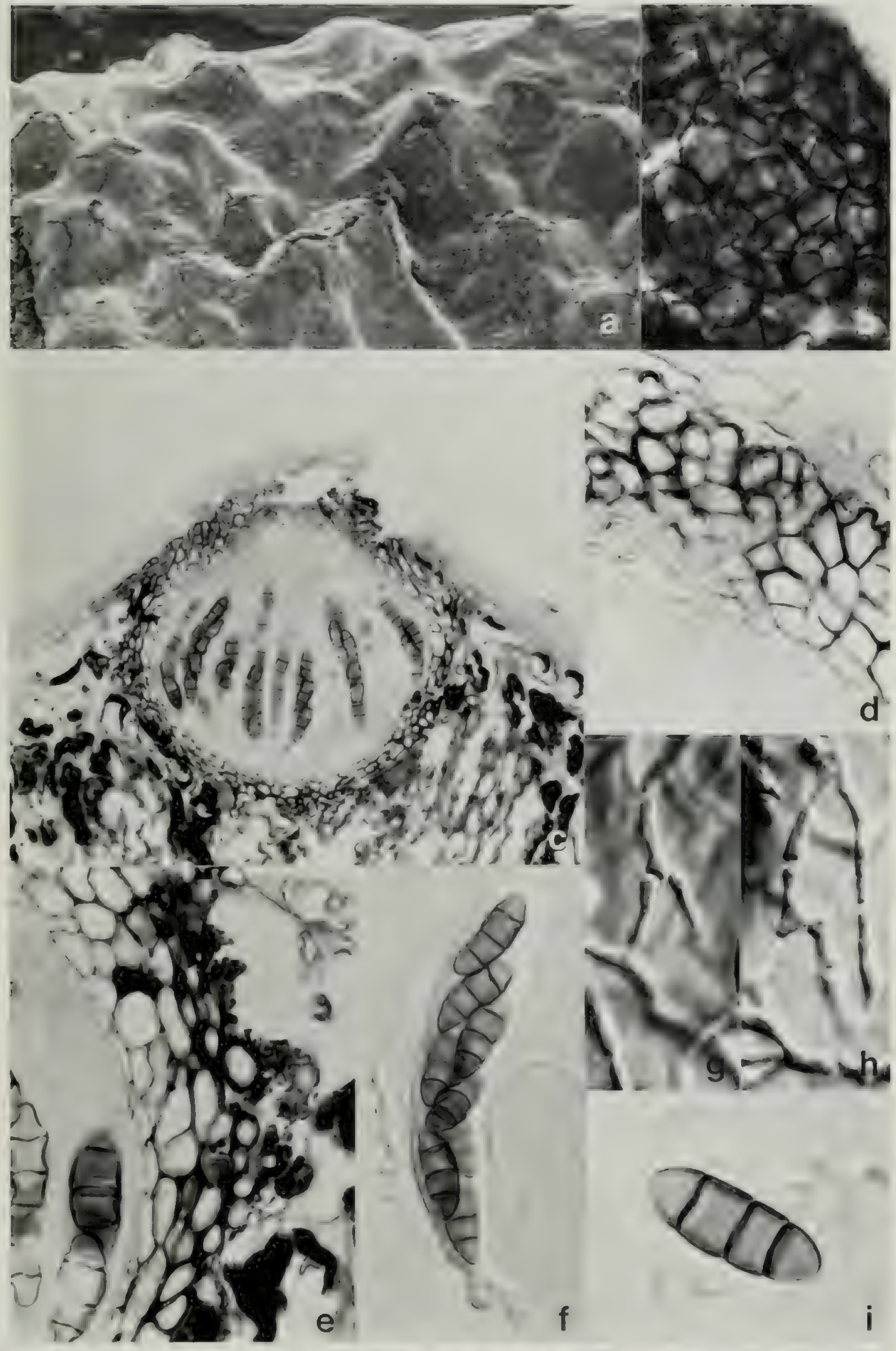

Figure 5. *Leptosphaeria cercocarpi*. a. SEM of immersed ascocarps, x50. b. ascocarp wall surface, x550. c. longitudinal median section through ascocarp, x225. d. section through ascocarp wall neck region, x950. e. longitudinal median section through ascocarp wall, x950. f. ascus, x525. g, h. cellular pseudoparaphyses, x2,000. i. ascospore, x1,150. All from holotype of *L. cercocarpi*.

Phaeosphaeriaceae

The species considered in this section all possess characteristics of the Phaeosphaeriaceae (Barr 1987a). Species in the Phaeosphaeriaceae are distinguished from those in the Leptosphaeriaceae by the smaller ascomatal size, the thin, soft ascocarp wall composed of pseudoparenchymatous cells, and the rather sparse pseudoparaphyses (Barr 1987a). The genera represented within the family are *Paraphaeosphaeria* Eriksson, *Phaeosphaeria* Miyake, and *Kalmusia* Niessl.

•*Paraphaeosphaeria concentrica* (J.B. Ellis & B.M. Everhart) S.M. Huhndorf comb. nov. See Figure. 6.

≡ *Leptosphaeria concentrica* J.B. Ellis & B.M. Everhart, The North American Pyrenomycetes. A Contribution to Mycologic Botany, p. 354. 1892. (Basionym).

Ascocarps scattered, sparse, immersed-subepidermal, globose, papillate, glabrous, 90–100 µm diameter, 100–125 µm high. **Ascocarp wall** of textura angularis in surface view; in longitudinal section 7.2–10.8 µm thick at sides and base, composed of 2–3 layers of elongate-compressed, hyaline, pseudoparenchymatic cells (2.8–3.6 x 12–14.5 µm), wall up to 13 µm thick near apex, composed of 3–4 layers of isodiametric-elongate, slightly brown-melanized cells (3.6–5.6 x 7.2–12.2 µm). **Papilla** very short, erumpent, bluntly conical, 15–20 µm high, 25–30 µm wide, 10–13 µm thick near base of papilla, papilla apex wall cells hyaline, thin-walled surrounding a circular ostiole without periphyses. **Pseudoparaphyses** 1.4–2.0 µm wide, 70–90 µm long (height of the ascocarp cavity), numerous, narrowly cellular, without gelatinous coating. **Asci** (43–)54–66 x 10.8–12.2 µm, numerous, basal, cylindrical-clavate, thick-walled, short-stalked, rounded apex, with apical chamber, with 8 biseriate ascospores. **Ascospores** (14.5–)16.5–18.7 x (3.6–) 4.3–5.7(–6.5) µm, cylindrical, with rounded end cells, end cells longer than central cell, straight; 2-septate, septa unevenly distributed, order of septation 2:1, primary septum submedian and constricted; brown, wall roughened, thin cellular sheath entirely surrounding spore, without appendages.

Holotype: United States: On apple leaves (*Malus* sp.), Columbia, Missouri (H. Dorsett), and Louisiana (Langlois) (NY).

Comments: *Paraphaeosphaeria* species are distinguished by ascocarps that form below or within the host epidermis, an ascocarp wall consisting of a few layers of pseudoparenchyma, and cylindrical, usually echinulate ascospores with the primary septum forming in the lower half of the spore.

Although *Paraphaeosphaeria* species are commonly found on monocotyledonous plants, species on dicot plants have also been placed in the genus (Hedjaroude 1969, Shoemaker and Babcock 1985). Such is the case here with *Paraphaeosphaeria concentrica* described from apple leaves. The description of *P. concentrica* closely resembles the description of the type of the genus, *P. michotii* (Westendorp) Eriksson, with the only difference being the dicotyledonous host plant. *Paraphaeosphaeria michotii* and its synonyms have so far been found exclusively on monocot hosts (Shoemaker and Eriksson 1967, Shoemaker and Babcock 1985). Overlooking substratum preference, *P. concentrica* would be synonymous with *P. michotii*. Because of the historical value placed on this character and the need for experimental evidence to demonstrate the range of substrata on which species will grow and the total lack of collections of *P. michotii* on dicot hosts, *P. concentrica* is retained as a separate species.

•*Phaeosphaeria pomona* (P.A. Saccardo) S.M. Huhndorf comb. nov. See Figure 7.

≡ *Leptosphaeria (Leptosphaerella) pomona* P.A. Saccardo, Nuovo Giornale Botanico Italiano e Bolletino della Società Botanica Italiana 8:176. 1876. (Basionym).

Ascocarps scattered, sparse, immersed-subcuticular, globose, papillate, glabrous to slightly tomentose near base, with loose, dark hyphal growth on host cuticle surrounding ascocarps, (55–)90–125 µm diameter, 75–115 µm high. **Ascocarp wall** of textura angularis-globulosa in surface view; in longitudinal section uniformly 6.1–7.7 µm thick, composed of 2–3 layers of brown-melanized, compressed, isodiametric-to-elongate pseudoparenchymatous cells (1.5–2.0 x 8–12 µm). **Papilla** very short, erumpent, bluntly conical, 15–21 µm

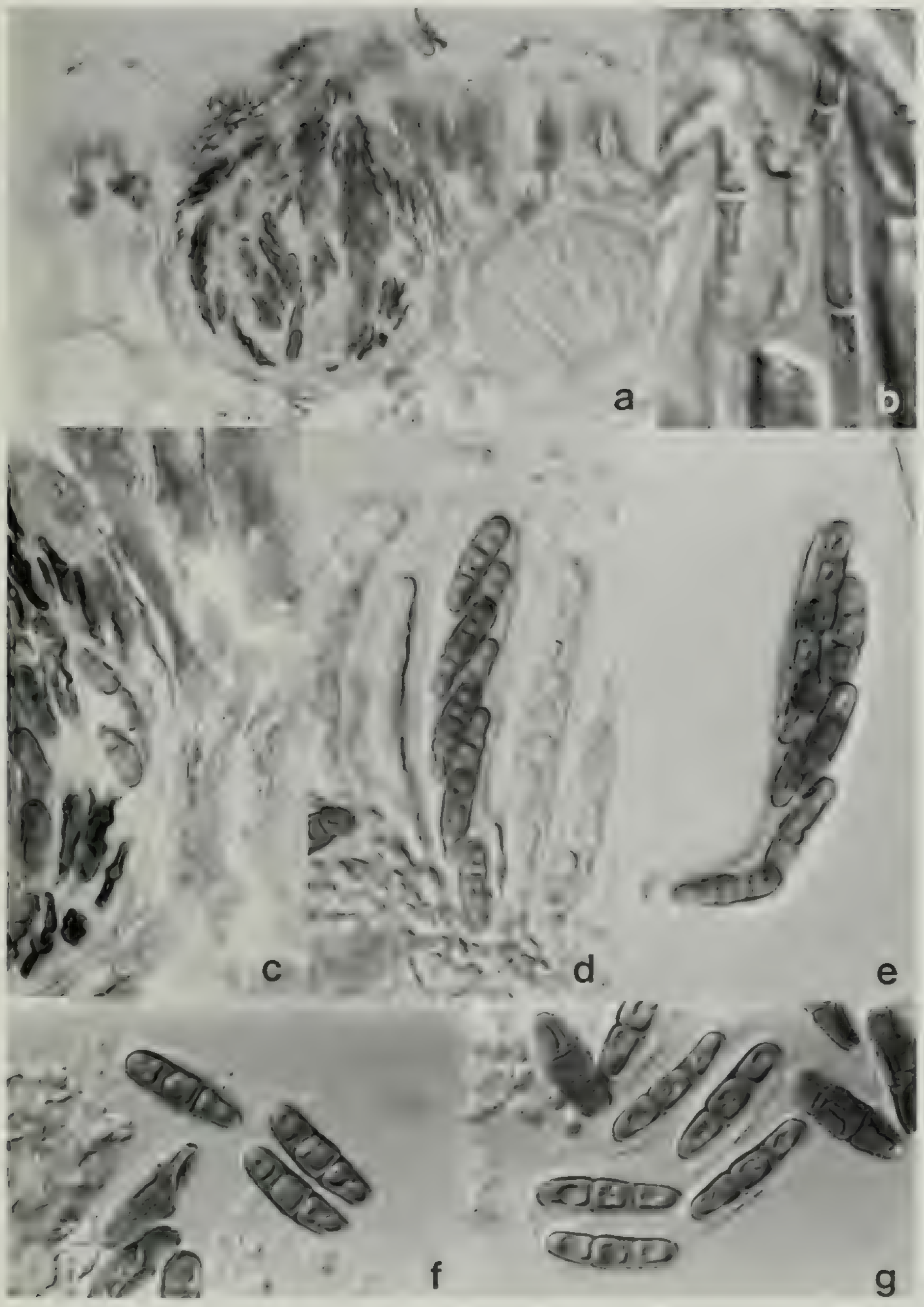

Figure 6. *Paraphaeosphaeria concentrica*. a. longitudinal median section through ascocarp, x375. b. cellular pseudoparaphyses, x2,000. c. longitudinal median section through ascocarp wall, x950. d, e. asci, x1,050. f, g. ascospores, x1,150. All from holotype of *P. concentrica*.

high, 31–37 µm wide, composed of 3–4 layers of small, brown-melanized, isodiametric cells (2.6–4.6 µm diameter), (9–)12–17 µm thick near base of papilla, apex of papilla wall cells hyaline, thin-walled surrounding a circular ostiole without periphyses. **Pseudoparaphyses** 1.0–1.5 µm wide, (46–)77–93 µm long (height of the ascocarp cavity), numerous, narrowly cellular, with guttule-like thickenings at septa, without gelatinous coating. **Asci** 55.5–65 x

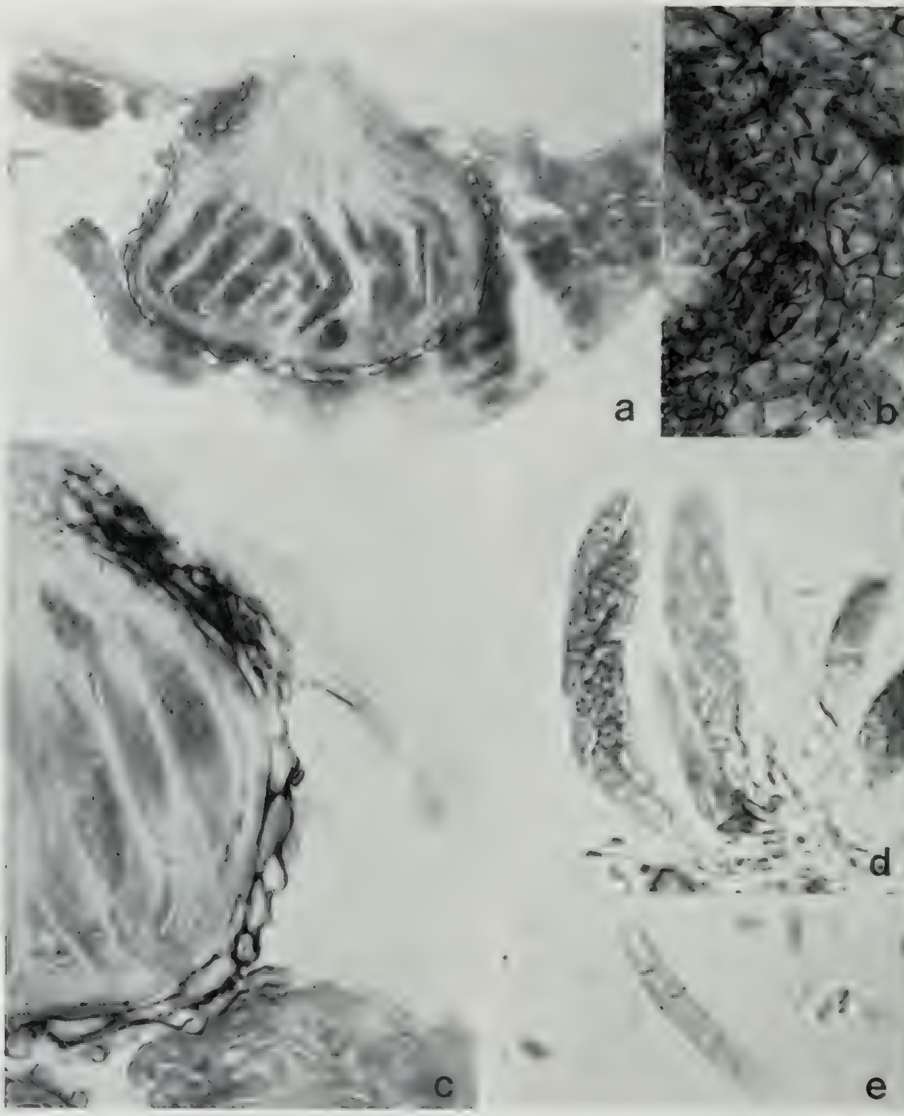

Figure 7. *Phaeosphaeria pomona*. a. longitudinal median section through ascocarp, x375. b. ascocarp wall surface, x550. c. longitudinal median section through ascocarp wall, x950. d. ascus, x1,050. e. ascospore, x1,150. All from holotype of *P. pomona*.

8.3–11.5 µm, numerous, basal, cylindrical, thick-walled, short-stalked, rounded apex, with apical chamber, with 8 biseriate ascospores. Ascospores 20.1–26.5 x (2.8–)3.6–5.0 µm, narrowly fusiform, with acute end cells, second cell from the top occasionally enlarged, straight; 5-septate, septa unevenly distributed, without constrictions, order of septation unknown, pale brownish yellow, guttules present in ascospore cells, smooth, thin cellular sheath entirely surrounding spore (0.7–2.0 µm thick).

Holotype: ITALY: In pag. super. folior. *Pyri Mali*, socia *Vermicularia Pomona*, a selva (Treviso), Sept. 1875, raro (PAD).

Comments: See under *Phaeosphaeria lucilla*.

•*Phaeosphaeria lucilla* (P.A. Saccardo) S.M. Huhndorf comb. nov. See Figure 8.

≡ *Leptosphaeria lucilla* P.A. Saccardo, Nuovo Giornale Botanico Italiano e Bolletino della Società Botanica Italiana 7:310-311. 1875. (Basionym).

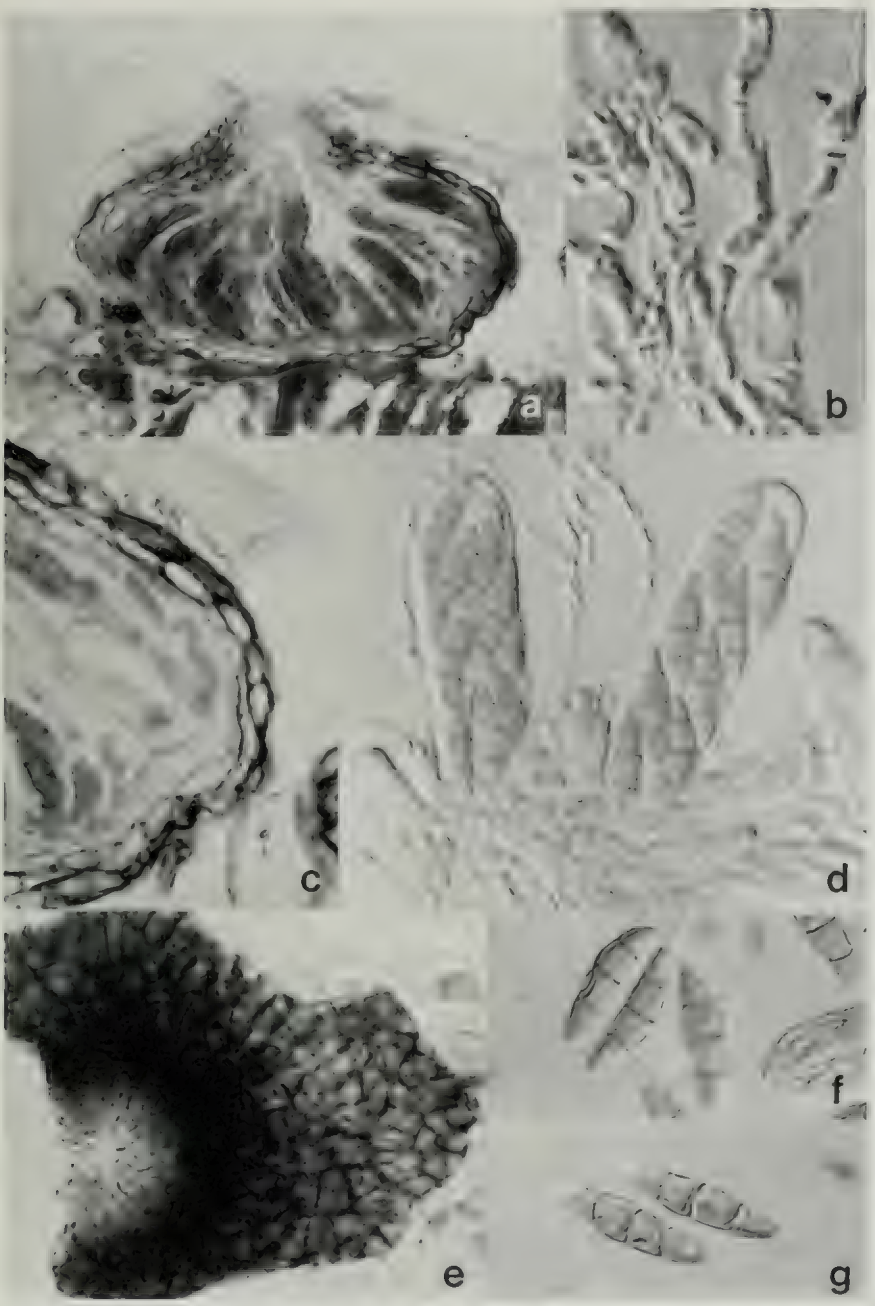

Figure 8. *Phaeosphaeria lucilla*. a. longitudinal median section through ascocarp, x375. b. cellular pseudoparaphyses, x2,000. c. longitudinal median section through ascocarp wall, x950. d. asci, x1,050. e. ascocarp wall surface, x550. f, g. ascospores, x1,150. All from holotype of *P. lucilla*.

Ascocarps scattered, sparse, immersed-subcuticular, papillate, glabrous, depressed-globose, 110–130 µm diameter, 90–115 µm high. **Ascocarp wall** of textura angularis in surface view; in longitudinal section uniformly 6.0–7.7 µm thick, composed of 3–4 layers of brown-melanized, compressed, isodiametric-to-elongate, pseudoparenchymatous cells (2.3–3.8 x 6.9–10.0 µm). **Papilla** very short, erumpent, conical, 20–25 µm high, 30–40 µm wide, composed of 4–5 layers of brown-melanized, isodiametric cells (3.0–4.6 µm diameter), 10.7–

.0 µm thick near base of papilla, apex of papilla wall cells hyaline, thin-walled surrounding a circular ostiole without periphyses. **Pseudoparaphyses** 1.5–2.0 µm wide, 62–71 µm long (height of the ascocarp cavity), numerous, narrowly cellular, without gelatinous coating. **Asci** 40–51(–56) x 8.4–10(–11.5) µm, numerous, basal, in a broad hymenium, cylindrical, thin-walled, sessile, rounded apex, with 8 bi- to triseriate ascospores. **Ascospores** 15.3–18.4(–20) x 3.0–4.6 µm, fusiform, with acute end cells, second cell from apex slightly enlarged, straight to slightly curved; 3-septate, septa evenly distributed, order of septation 2:1:2, primary septum median and slightly constricted; pale yellowish brown, wall smooth, without sheath or appendages.

Holotype: ITALY: In foliis languidis *Pyri communis* in agro Tarvisino et Patavino (PAD).

Comments: Fungi in the genus *Phaeosphaeria* are characterized by immersed ascocarps with thin walls of pseudoparenchyma, fusiform 3- to multiseptate ascospores and monocotyledonous hosts. Nonetheless, Leuchtmann's (1984) treatment of *Phaeosphaeria* includes a group of species found on the leaves and stems of plants in the dicot family Caryophyllaceae. The placement of dicotyledonous *Leptosphaeria* species, morphologically similar to *Phaeosphaeria*, into the genus *Phaeosphaeria* is contrary to Shoemaker and Babcock's (1989b) concept of the genus. These authors do not, however, suggest an alternative genus for these species. They do place certain species on dicots in *Leptosphaeria*, citing the presence of thick-walled cells in the ascocarp wall. *Phaeosphaeria pomona* and *P. lucilla* are morphologically similar to species of *Phaeosphaeria* found on monocot hosts. They do not have the ascocarp and wall characteristics of *Leptosphaeria*.

When *P. pomona* and *P. lucilla* were described, Saccardo (1875, 1876) placed them in *Leptosphaeria* subgenus *Leptosphaerella* Sacc., which included fungi from leaves of dicotyledonous plants. *Leptosphaeria* subgenus *Leptosphaerella* was subsequently placed in synonymy with *Phaeosphaeria* (Leuchtmann 1984). At this time, there is no other genus suitable for the placement of these "dicot *Phaeosphaeria*" species. Erecting a new genus for these species based solely on substrate preference, with no morphological differences from *Phaeosphaeria* seems unwise. With proof of strict substrate preference requiring experimental evidence, there seems to be some justification for their placement within *Phaeosphaeria* until such work is done.

•*Phaeosphaeria thomasiana* (P.A. Saccardo & C. Roumeguère) S.M. Huhndorf comb. nov. See Figure 9.

≡ *Leptosphaeria thomasiana* P.A. Saccardo & C. Roumeguère, Revue Mycologique 5:236. 1883. (Basionym).

Ascocarps scattered, numerous, immersed-subcuticular, globose, flattened at base, papillate, glabrous, 150–175 µm diameter, 110–125 µm high. **Ascocarp wall** of textura angularis-globulosa in surface view; in longitudinal section uniformly 9.3–12.2 µm thick, composed of 4–5 layers of polygonal, pseudoparenchymatous cells, outer 2–3 layers of polygonal-to-elongate, brown-melanized cells (2.2–5.0 x 6.5–8.6 µm), inner 1–2 layers of elongate-compressed, hyaline cells (0.7–1.5 x 8.0–10.8 µm). **Papilla** very short, erumpent, bluntly conical, 12–30 µm high, 10–36 µm wide, composed of 7–8 layers of small, brown-melanized, isodiametric cells (2.6–4.6 µm diameter), 14–18 µm thick near base of papilla, apex of papilla wall cells hyaline, thin-walled surrounding a 12–18 µm wide circular ostiole without periphyses. **Pseudoparaphyses** 1.0–1.5 µm wide, 80–85 µm long (height of the ascocarp cavity), numerous, narrowly cellular, without gelatinous coating. **Asci** 55.5–65.5 x 8.0–10.8 µm, numerous, basal, cylindrical-clavate, thick-walled, short-stalked, rounded apex, with apical chamber, with 8 biseriate ascospores. **Ascospores** 15.0–18 x 3.6–4.5 µm, fusiform, with acute end cells, straight or slightly curved; 3-septate, septa evenly distributed, order of septation 2:1:2, primary septum median, without constrictions; subhyaline to pale brownish yellow, guttules absent in ascospore cells, smooth, without sheath or appendages.

Holotype: FRANCE: In sarmentis *Rubi* emortuis (305-Reliquiae Libertianae) n.v.

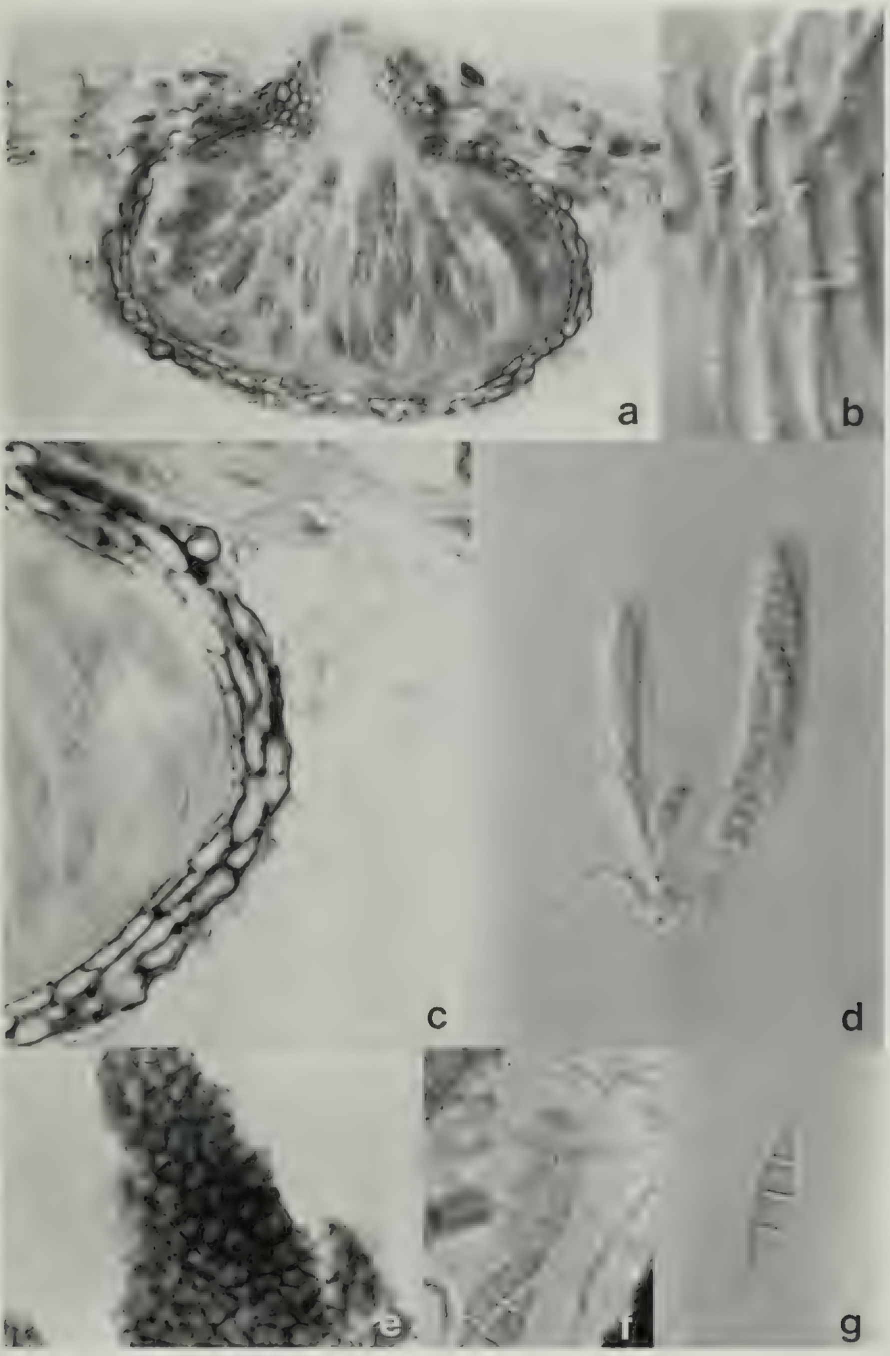

Figure 9. *Phaeosphaeria thomasiana.* a. longitudinal median section through ascocarp, x375. b. cellular pseudoparaphyses, x2,000. c. longitudinal median section through ascocarp wall, x950. d. asci, x1,050. e. ascocarp wall surface, x550. f, g. ascospores, x1,150. All from Roum. F. sel exs. 6039.

[Exsi]ccatae: FRANCE: Bois des Roches (Noidan), May 1891, F. Fautrey, Roumeguère, F. sel exs. 6039 (NY).

Other material examined: UNITED STATES: OREGON: Corvallis, on loganberry (*Rubus loganobaccus* Bailey), Mar. 12, 1930, S.M. Zeller; on loganberry, Mar. 15, 1916, A. Frank (all NY).

Comments: *Leptosphaeria thomasiana* is placed in *Phaeosphaeria* because of its small ascocarps immersed beneath the host cuticle and its ascocarp wall of pseudoparenchymatous cells. I was unable to see the type specimen, which is number 305 in the exsiccatae set Reliquiae Libertianae. This is not a regular exsiccatae set (Pfister 1985), and the set at FH did not contain this specimen. The description and plate herein were prepared from Roumeguère, F. sel exs. 6039 specimen from NY, which included few ascocarps. I did not find any ascocarps of *P. thomasiana* in the collections from Oregon, but the canes did have large gray patches on them as Zeller (1927) described. He also mentions that a cane blight or "Loganberry gray bark disease" has been ascribed to this organism in western Washington. I have seen no reports from other regions of this organism as a pathogen of *Rubus*.

•*Kalmusia clivensis* (M.J. Berkeley & C.E. Broome) M.E. Barr, Mycotaxon. An International Journal Designed to Expedite Publication of Research on Taxonomy & Nomenclature of Fungi & Lichens 29:504. 1987. See Figure 10.

≡ *Sphaeria (Caulicolae) clivensis* M.J. Berkeley & C.E. Broome, Annals and Magazine of Natural History, Series 2, 9:379. 1852.

≡ *Leptosphaeria clivensis* (M.J. Berkeley & C.E. Broome) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:16. 1883.

≡ *Diapleella clivensis* (M.J. Berkeley & C.E. Broome) A. Munk, Dansk Botanisk Arkiv 15(2):75. 1953.

= *Leptosphaeria galiorum* P.A. Saccardo var. *lapsanae* P.A. Saccardo & P.A. Briard, Revue Mycologique 7:209. 1885.

= *Leptosphaeria steironematis* J.B. Ellis & B.M. Everhart, Proceedings of the Academy of Natural Sciences of Philadelphia 1890: 237. (1890) 1891.

= *Leptosphaeria arunci* S.M. Zeller, Mycologia 19:134–135. 1927.

= *Leptosphaeria longipedicellata* J.H. Miller & G. Burton, Mycologia 34:2–3. 1942.

Ascocarps scattered, sparse, immersed-subepidermal, papilla erumpent, at times with a surrounding clypeus, glabrous, depressed-globose, 275–400 µm diameter, 175–375 µm high. **Ascocarp wall** of textura prismatica in surface view; in longitudinal section uniformly 15–20 µm thick, composed of 5–6 layers of parallel, elongate, prismatic, scleroplectenchymatic cells (0.7–1.5 x 15–20 µm), outer 3–4 cell layers slightly brown-melanized, inner 2–3 layers hyaline; at the base cells are compressed, flattened, hyaline. **Papilla** conical, short-intermediate, (50–)90–100(–130) µm high, 40–80 µm wide at the apex, 50–100 µm wide at the base, composed of 6–8 layers of small, light-brown pigmented, isodiametric cells with no external, melanized crust (2–5 µm diameter), 10–13 µm thick, surrounding a circular ostiole 18–20 µm wide, composed of thin-walled, hyaline, compressed cells, without periphyses. **Pseudoparaphyses** 0.5–1.5 µm wide, 200–225 µm long (height of the ascocarp cavity), numerous, narrowly cellular, without gelatinous coating. **Asci** 95–110(–150) x 11–15(–21) µm, numerous, basal, clavate, thin-walled, long-stalked (27–39 µm long), rounded apex, with 8 biseriate ascospores. **Ascospores** 19–25(–32) x 5–8.5(–11) µm, fusiform, with rounded to acute end cells slightly longer than central cells, straight to slightly curved; 3-septate, septa slightly unevenly distributed, order of septation 2:1:2, with slight constrictions at all septa; dark brown, smooth, without sheath or appendages.

Holotype: GREAT BRITAIN: King's Cliffe, on dead stems of *Pastinaca sativa*, Jul 1850, Herb. Berk. 1879 (K).

Exsiccatae: CANADA: London, on *Steironema ciliatum*, as *Leptosphaeria steironematis*, May 1890, Ell. & Ev., North American Fungi 2615 (NY); Sphaer. Brit. III 60, (FH).

Other material examined: CANADA: London, on *Steironema ciliatum*, May 1890, with 1640, Dearness (Holotype of *Leptosphaeria steironematis*, NY); 1640, London, as *Leptosphaeria steironematis*, 19 Apr., 1890

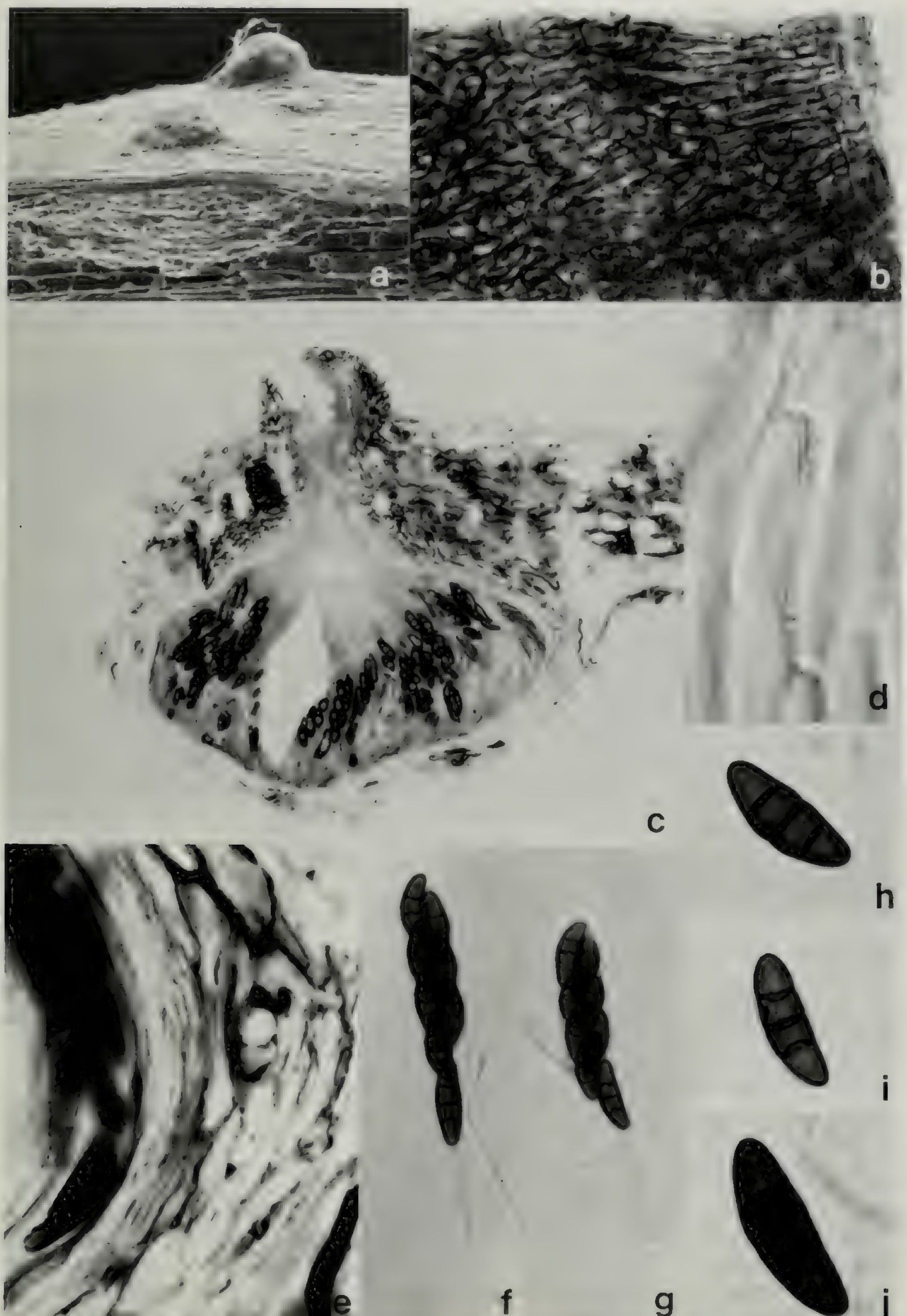

Figure 10. *Kalmusia clivensis*. a. SEM of immersed ascocarps with erumpent papilla, x100. b. ascocarp wall surface, x550. c. longitudinal median section through ascocarp, x125. d. cellular pseudoparaphyses, x2,000. e. longitudinal median section through ascocarp wall, x950. f, g. asci, x525. h–j. ascospores, x1,150. a, c, d, e, f, and h from holotype of *Leptosphaeria arunci*; b, g, and i from holotype of *K. clivensis*; j from lectotype of *L. longipedicellata*.

NY). GREAT BRITAIN: England, Chute Meadow, Lambriggan, W. Cornwall, on *Centaurea nigra*, May 9, 1942, F. Rilstone (NY-MEBB coll); Scotland, Wester Ross, Rassal N.N. Reserve, on ? *Senecio jacoboea*, June 2, 1982, P.F. Cannon (NY). ITALY: Briard no. 8, on *Lapsana communis*, June 12, 1885 (holotype of *Leptosphaeria galiorum* var. *lapsanae*, PAD). UNITED STATES: COLORADO: Larimer Co., 3 mi W. Redfeather Lakes, 8100' Roosevelt National Forest, on *Rosa* sp., Aug. 4, 1984, MEBB # 7008 (NY); GEORGIA: 7684, Clarke Co., Athens, South Campus, University of Georgia, on *Daucus carota*, Sept. 11, 1939, J.H. Miller (Lectotype of *Leptosphaeria longipedicellata*, GAM); MICHIGAN: Emmet Co., Gill and Elder Roads, Carp Lake, on ? *Acer*, Sept. 11, 1969, MEBB #5527 (NY); OREGON: Multnomah Falls, April, on dead stems of *Aruncus silvester* (holotype of *Leptosphaeria arunci* in Zeller Herb. 6811, NY).

Comments: Four of the putative *Leptosphaeria* species that were examined are synonymous with *Kalmusia clivensis*; one was found on a Rosaceous host (*L. arunci* on *Aruncus*). The most distinctive feature of this species is the presence of long-stipitate asci with prominent dark brown, 3-septate ascospores. The long stipe, as well as the thin ascus wall, has led previous workers to treat it as a unitunicate fungus in the monotypic genus *Diapleella* (Munk 1957, Dennis 1978). Shoemaker (1984a) retained the genus *Diapleella* but treated it as bitunicate. Barr (1987b) transferred *D. clivensis* to the genus *Kalmusia* Niessl without much explanation. The original description of *Kalmusia* (Niessl 1871) and the illustration of the genus in Berlese (1890) show a fungus with long-stipitate asci and dark brown, 3-septate ascospores. *Kalmusia clivensis* appears to be well-placed within this genus.

Shoemaker (1984a) looked at one collection of *Leptosphaeria longipedicellata* on *Solidago caesia* L., which is cited in the original description of the species. He mentions that "the original description of *L. longipedicellata* is strongly suggestive of *Diapleella clivensis*." This collection was in fact *L. macrospora* (Fuckel) Thümen, and Shoemaker did not resolve the placement of *L. longipedicellata*. The collection on *Daucus carota* L., cited in the description and marked as type on the herbarium packet, matches the original description exactly and is the same as *Kalmusia clivensis* except that the ascospores and asci are slightly larger than those in the type collection of *K. clivensis*. The ascocarp and wall in section appear exactly the same. I believe the size differences are probably due to environmental differences or other individual variation and that *L. longipedicellata* is synonymous with *K. clivensis*. Collection 7684, Clarke Co., Athens, South Campus, University of Georgia, on *Daucus carota*, Sept. 11, 1939, J.H. Miller (GAM) is chosen as the lectotype of *Leptosphaeria longipedicellata*.

•*Kalmusia coniothyrium* (L. Fuckel) S.M. Huhndorf comb. nov. See Figure 11.

≡ *Sphaeria coniothyrium* L. Fuckel, Symbolae Mycologicae, p. 115. 1870. (Basionym).

≡ *Leptosphaeria coniothyrium* (L. Fuckel) P.A. Saccardo, Nuovo Giornale Botanico Italiano e Bolletino della Società Botanica Italiana 7:317. 1875.

≡ *Melanomma coniothyrium* (L. Fuckel) L. Holm, Symbolae Botanicae Upsalienses 14(3):56–57, 1957.

≡ *Diapleella coniothyrium* (L. Fuckel) M.E. Barr *in* M.E. Barr, C.T. Rogerson, S.J. Smith, and J.H. Haines, Bulletin of the New York State Museum 459:30. 1986.

= *Sphaeria (Obtectae) hendersonia* J.B. Ellis *in* M.C. Cooke and J.B. Ellis, Grevillea 6:14–15. 1877.

≡ *Clypeosphaeria hendersoniae* (J.B. Ellis) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:91. 1883.

≡ *Leptosphaeria (Clypeosphaeria) hendersoniae* (J.B. Ellis) M.C. Cooke, Grevillea 17:91. 1889.

Ascocarps clustered, numerous, immersed-subepidermal, depressed, globose, flattened at top and base, sometimes beneath blackened clypei, papillate, glabrous, 175–300 µm diameter, 175–200 µm high. **Ascocarp wall** of textura angularis-globulosa in surface view; in longitudinal section 15–25 µm thick at the sides, 13–18 µm at the base, composed of 8–12 layers of polygonal, pseudoparenchymatous cells, outer 3–5 layers of isodiametric-to-slightly-elongate, light brown cells (5.0–9.5 x

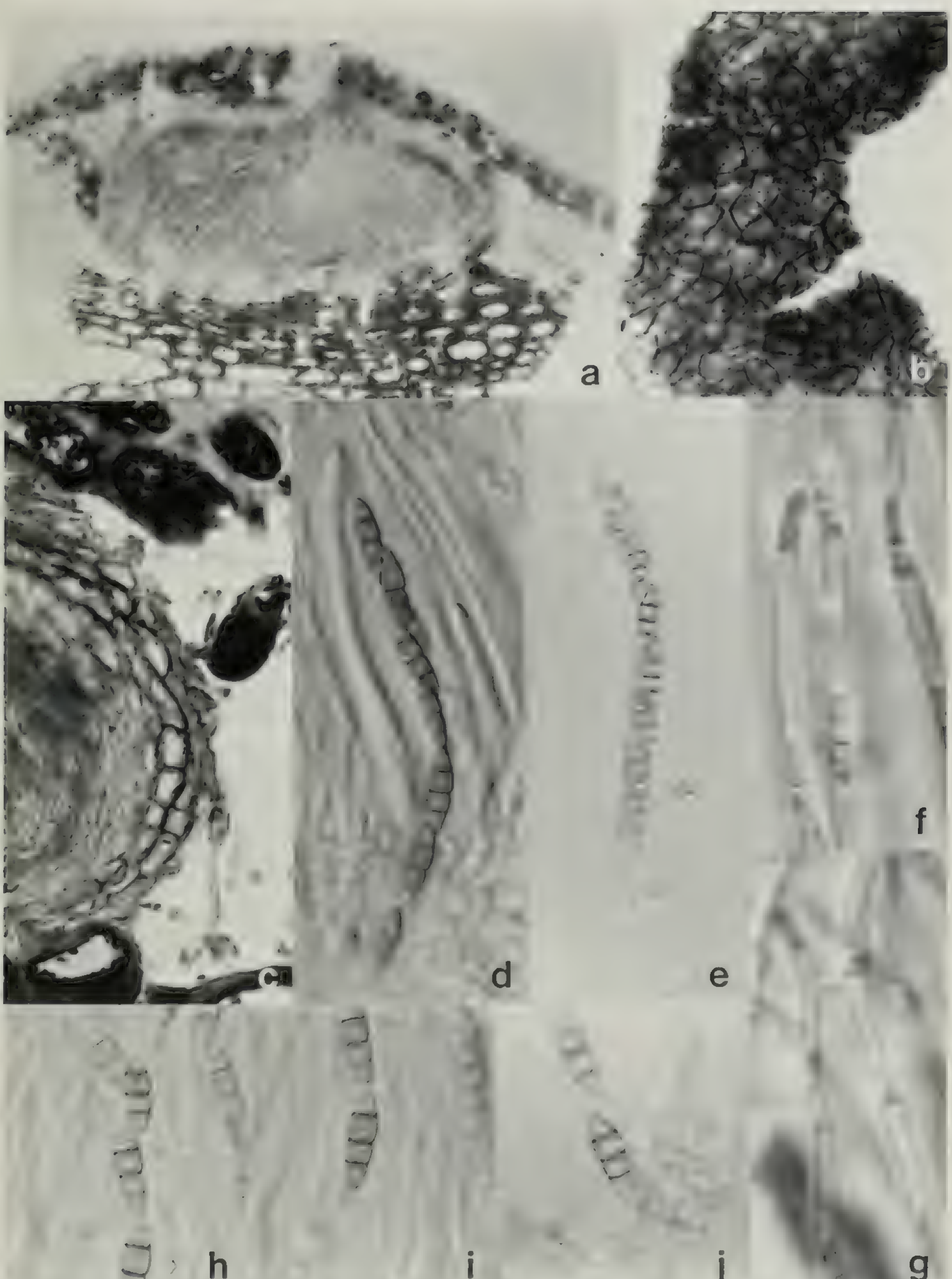

Figure 11. *Kalmusia coniothyrium*. a. longitudinal median section through ascocarp, x250. b. ascocarp wall surface, x550. c. longitudinal median section through ascocarp wall, x950. d, e. asci, x1,050. f, g. cellular pseudoparaphyses, x2,000. h–j. ascospores, x1,150. a–d, f–i from holotype of *K. coniothyrium*; e, j from neotype of *Sphaeria hendersonia*.

3.6–5.0 µm), inner 5–7 layers of small, isodiametric-elongate, compressed, hyaline cells (3.6–4.3 x 2.0–3.6 µm). **Papilla** short, erumpent, bluntly conical, 45–55 µm high, 25–35 µm wide, 16–18 µm thick, composed of 5–10 layers of small, hyaline, isodiametric cells (1.4–2.8 µm diameter), surrounding a 10–20 µm wide, circular ostiole without periphyses. **Pseudoparaphyses** 1.0–1.5 µm wide, 75–100 µm long (height of the ascocarp cavity), numerous, narrowly cellular, with guttule-like thickenings at septa, with gelatinous coating. **Asci** 60–75 x 5.5–7.5 µm, numerous, basal in a broad hymenium, cylindrical, thin-walled, short-stalked, rounded apex, with apical chamber, with 8 overlapping, uniseriate ascospores. **Ascospores** 11.5–14.4(–15.8) x 3.6–4.5 µm, fusiform to ellipsoidal, with acute end cells, second cell somewhat enlarged, straight or slightly curved; 3-septate, septa slightly unevenly distributed, order of septation 2:1:2, primary septum median and constricted; brownish yellow, guttules lacking, smooth, without sheath or appendages.

Holotype: AUSTRIA: Auf durren Ranken von *Rubus fruticosus*, selten, im Fruhling. An der Heimbach bei Oestrich (G).

Exsiccatae: Rehm, Asc. 388, on *Rubus fruticosus* (NY); Krieger, Fungi saxon. 18, 1120, 1121 (NY); Petrak Kryptogamae exsic. 2318 (NY); Sacc, Mycotheca Veneta 72, as *Sphaeria fuscella* f. *Ampelopsidis hederaceae*, (FH); Petrak, Fl. Boh. et Mor. exsic. II no. 4, as *Clypeosphaeria notarisii* (FH); Ellis N. American Fungi 581 as *Sphaeria Hendersonia*, Mar. 1878 (ILL, FH, NY).

Other material examined: CANADA: Ottawa, on Sambucus racemosa, Mar. 10, 1897 (NY); London, as *Clypeosphaeria Hendersonia*, 1883, 3 May 1892 (NY). ITALY: 198 as *Sphaeria clypeata*, de Notaris (RO). UNITED STATES: DELAWARE: Faulkland, as *Sphaeria Hendersonia*, Mar. 20, 1887 (NY); NEW JERSEY: Newfield, on *Rubus strigosus*, J.B. Ellis 101, May 29, 1880 (neotype of *Sphaeria Hendersonia*, NY); on *Rubus occidentalis*, as *Sphaeria Hendersonia*, Aug. 4 1879, Apr. 1880, J.B. Ellis (FH); as *Clypeosphaeria Hendersonia*, Aug. 15, 1894, J.B. Ellis 773 (NY); MASSACHUSETTS: Andover, as *Sphaeria Hendersonia*, Rev. J. Blake No. 79 (NY); NORTH DAKOTA: Kulm, on Rubus strigosus, Mar. 12, 1916, Brenkle, Fungi Dakotenses 384 (NY); OREGON: Troutdale, Feb. 10, 1929, M.J. O'Connell (NY); Gresham, Apr. 30, 1934, S.M. Zeller (NY); PENNSYLVANIA: Avestrud Co., on *Rubus* sp., July 10, 1944 (NY); WISCONSIN: Sauk Co., Aldo Leopold Reserve, on *Rubus* sp., 9 Apr. 1988, 30 Sept. 1988, S.M. Huhndorf (ILLS).

Comments: This fungus is placed in *Kalmusia* because of its immersed, clypeate ascocarps with pseudoparenchymatous walls composed of compressed cells. *Kalmusia coniothyrium* lacks the characters distinctive of *Leptosphaeria*, including erumpent to superficial ascocarps with a wall of scleroplectenchymatous cells. Holm (1957) placed the species in *Melanomma*, but the fungus does not fit the current concept of that genus (Barr 1987a) because it lacks erumpent ascocarps with walls composed of small thick-walled cells, asci formed peripherally within the centrum, and trabeculate pseudoparaphyses. However, the ascospores of this fungus do strongly resemble those of some *Melanomma* species. The ascus shape of *K. coniothyrium* differs from that of *K. clivensis* in being cylindrical and short-stalked, and the ascospores are brownish yellow rather than dark reddish brown. But in *Kalmusia ebuli* Niessl, the type of the genus, these characters are variable; asci are clavate to cylindrical, short- or long-stalked, and ascospores are lighter brown than those of *K. clivensis*. There appears to be sufficient range within the genus to accommodate *K. coniothyrium*.

Sphaeria hendersonia is synonymous with *K. coniothyrium*. The description for the holotype specimen is at NY, but the actual specimen is missing. Because no other specimen is cited in the published description and it is uncertain what was available to Ellis when he described the organism, a neotype was chosen from the Ellis collection at NY which matches the description and is in good condition. The neotype of *Sphaeria hendersonia* is J.B. Ellis 101, Newfield, New Jersey, on *Rubus strigosus*, May 29, 1880.

Lophiostomataceae

The following species possesses characteristics of the Lophiostomataceae in the order Pleosporales (Barr 1987a). Lophiostomataceae *sensu* Holm and Holm (1988) is considered a heterogeneous group whose overall common characters, the flattened neck and slotlike ostiole, are highly adaptive and unstable. Consequently, the family in this sense may be completely dissociated (Holm and Holm 1988). Lophiostomataceae *sensu* Barr (1987a) contains genera that are united by wall characteristics, pseudoparaphysis structure and ascospore morphology. The compressed apical papilla is considered to be of generic or specific importance. Taxa in the Lophiostomataceae may have this type of papilla or may have a conspicuous, rounded apical papilla, or a short papilla with or without grouped setae, or the apex may open by a pore or slit.

•*Lophiostoma subcutanea* (M.C. Cooke & J.B. Ellis) S.M. Huhndorf comb. nov. See Figure 12.

≡ *Sphaeria (subtectae) subcutanea* M.C. Cooke & J.B. Ellis, Grevillea 7:41. 1878. (Basionym).
≡ *Leptosphaeria subcutanea* (M.C. Cooke & J.B. Ellis) J.B. Ellis *in* N.L. Britton, Catalogue of Plants Found in New Jersey. Geological Survey of New Jersey, Final Report of the State Geologist, 2(1):525. 1889.
≡ *Metasphaeria subcutanea* (M.C. Cooke & J.B. Ellis) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:167. 1883.

Ascocarps clustered, sparse, superficial, papillate, glabrous, conic, 150–170 µm diameter, 180–225 µm high. **Ascocarp wall** of textura angularis-prismatica in surface view; in longitudinal section (15–)20–23 µm thick at sides and base, composed of 6–7 layers of polygonal, isodiametric-to-elongate, pseudoparenchymatic cells (2.0–3.6 x 5–7 µm), outer 3–4 layers of brown-melanized cells at the sides, inner 1–3 layers of hyaline, compressed cells; basal wall composed only of hyaline, elongate-compressed cells. **Papilla** elongate-conical, longitudinally compressed, 75–85 µm high, 55–75 µm wide at the apex, 100–125 µm wide at the base, composed of 6-7 layers of brown-melanized, thickened, isodiametric cells (2.5–4.0 µm diameter); at apex, cells coalescing to form a thickened dark brown mass; wall 25–27 µm thick, surrounding a 40–50 µm wide slotlike ostiole lined with periphyses. **Pseudoparaphyses** 0.5–1.5 µm wide, 108–124 µm long (height of the ascocarp cavity), numerous, narrowly cellular, without gelatinous coating. **Asci** 77–84(–92) x 5.3–7.6 µm, numerous, basal, cylindrical, thin-walled, short-stalked, rounded apex, with 8 biseriate ascospores. **Ascospores** (20–)25–29 x 3.0–3.5 µm, narrowly fusiform, with acuminate end cells, second cell slightly enlarged, straight to slightly curved; 4-6(-8)-septate, septa unevenly distributed, order of septation unknown, with slight constrictions at all septa; hyaline to subhyaline, guttules present in ascospore cells, wall smooth, possibly with thin cellular sheath surrounding entire spore, without appendages.

Holotype: UNITED STATES: On decorticated limbs of *Pyrus communis* L (NY, K).

Comments: Holm and Holm (1988) considered the Swedish species of the Lophiostomataceae and emphasized ascocarp shape and peridial anatomy in distinguishing the genera *Lophiostoma* Ces. & de Not. and *Lophiotrema* Sacc. emend. L. Holm & K. Holm. The presence of a flattened papilla or neck and a slotlike ostiole have been used to distinguish the Lophiostomataceae from other groups. Although these features are highly variable in some species, they are still useful for placing this species in the Lophiostomataceae. However, generic placement within the family is problematic. The conic or pyriform ascocarp shape with a distinct flattened neck and the fusiform ascospores that are multiseptate within the ascus suggest *Lophiostoma*. The cylindric asci suggest *Lophiotrema*. The ascocarp wall anatomy in section resembles that of *Lophiotrema*, with uniformly thick walls of polygonal globose or angular cells. But in surface view, the cells seem to form a textura prismatica suggesting the long, parallel cells of *Lophiostoma*. The fungus is placed in *Lophiostoma* with some reservation because, at this time, there is no other suitable place for it.

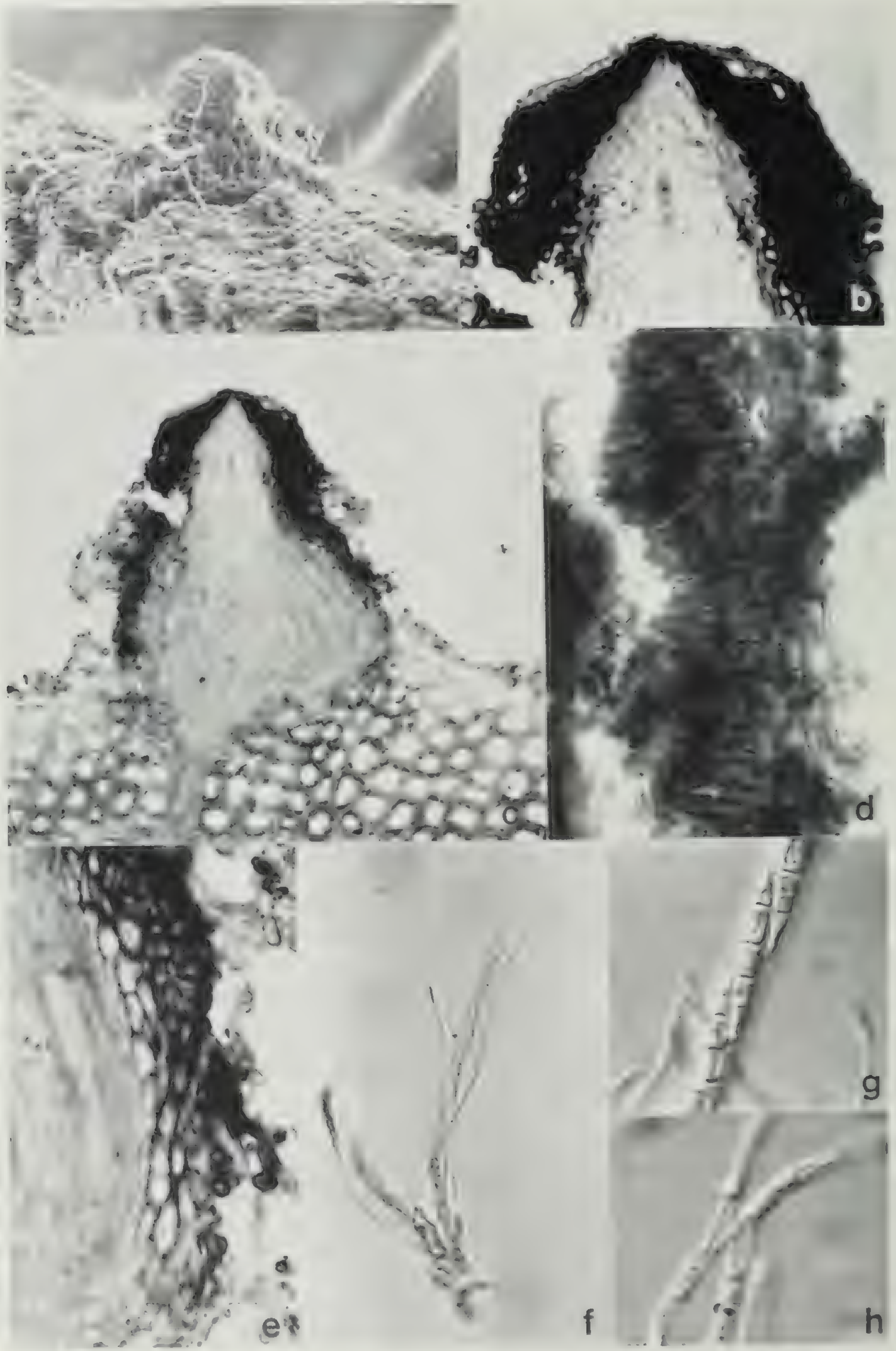

Figure 12. *Lophiostoma subcutanea*. a. SEM of ascocarp with apical crest, x175. b. longitudinal section of ascocarp neck with periphyses, x525. c. longitudinal median section through ascocarp, x325. d. ascocarp wall surface, x550. e. longitudinal median section through ascocarp wall, x950. f. ascus, x525. g. ascospores [illegible], x1,150. h. cellular pseudoparaphyses, x2,000. All from holotype of *L. subcutanea*.

Leptosphaeria Species Referable to the Melanommatales

One species investigated had characteristics of the Melanommataceae in the order Melanommatales (Barr 1987a). The order Melanommatales is distinguished from the Pleosporales by trabeculate pseudoparaphyses, asci arranged peripherally within the centrum, an ascocarp wall composed of small or compressed cells, and ascospores with bipolar symmetry. Any one of these features may deviate in a particular taxon. Fungi in the Melanommataceae are distinguished by gregarious, erumpent ascocarps with a wall of small, thick-walled cells.

•*Melanomma pulvis-pyrius* (C.H. Persoon:E.M. Fries) L. Fuckel, Symbolae Mycologicae p. 159, 1870. See Figure 13.

≡ *Sphaeria pulvis-pyrius* C.H. Persoon, Synopsis Methodica Fungorum p. 86, 1801; E.M. Fries, Systema Mycologicum Sistens Fungorum 2:458. 1823.

= *Cladosphaeria rimicola* G.H. Otth, Mitteilungen der Naturforschenden Gesellschaft in Bern 1870:106. 1871. Nom inval. Art. 43.1. [The genus *Cladosphaeria* was validated in 1894.]

≡ *Leptosphaeria rimicola* (G.H. Otth) P.A. Saccardo, Hedwigia, Dresden 35:XXIX. 1896; Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 11:XXIX. 1896.

Ascocarps clustered, sparse, superficial, papillate, glabrous with tomentum of thick-walled brown hyphae surrounding and between ascocarps, conic-subglobose to irregular, 425–550 µm diameter, 475–600 µm high. **Ascocarp wall** of textura angularis-epidermoidea in surface view; in longitudinal section 55–75 µm thick at sides, 80–100 µm thick at base, composed of 21–35 layers of cells, outer 5–6 layers of polygonal, isodiametric, brown-melanized, scleroplectenchymatic cells (3.6–4.3 x 7–8 µm) giving rise to the thick-walled hyphae of the tomentum, middle 6–9 layers composed of hyaline, polygonal-elongate, scleroplectenchymatic cells (5–7 x 10–12 µm), inner 10–20 layers of small, polygonal, thick-walled, hyaline cells (2.0–5.7 µm diameter), which become compressed and obscured toward the interior of the cavity. **Papilla** broadly rounded to dome-shaped, 110–160 µm high, 160–250 µm wide at the apex, 220–300 µm wide at the base; wall 36–54 µm thick, composed of 12–15 layers of cells, outer layers of brown-melanized, thickened, isodiametric cells (3.6–5.7 µm diameter), inner layers hyaline, compressed, surrounding a 75–150 µm wide circular ostiole lined with periphyses. **Pseudoparaphyses** 0.5–1.5 µm wide, 250–375 µm long (height of the ascocarp cavity), numerous, trabeculate with sparse branching, with guttule-like thickenings at septa, without gelatinous coating. **Asci** (95–)120–150 x 8.5–12 µm, numerous, basal and lateral, partially lining the peripheral wall of the centrum, cylindrical, thin-walled, short-stalked, rounded apex, with 8 overlapping uniseriate ascospores. **Ascospores** 17.2–22.3 x 5.7–8.0 µm, fusiform, with acute end cells, straight to slightly curved; 3-septate, septa evenly distributed, order of septation 2:1:2, primary septum median and slightly constricted, bipolarly asymmetrical with a wider anterior and a narrower posterior part, second cell slightly enlarged; pale brown occasionally with slightly lighter colored end cells, wall smooth, without sheath or appendages.

Exsiccatae: Czechoslovakia: Betschwa-Ufer, Dec. 27, 1911, M. Weisskirchen, Petrak, Fl. Boh et Mor. exsic. Lfg. 4 Nr. 196 (FH); Finland: Bjork, Dec. 9, 1865, Karsten, Fungi Fenniae 992 (FH); Finland: on *Sambucus racemosa*, Jan. 1866, Karsten, Fungi Fenniae 995 (FH).

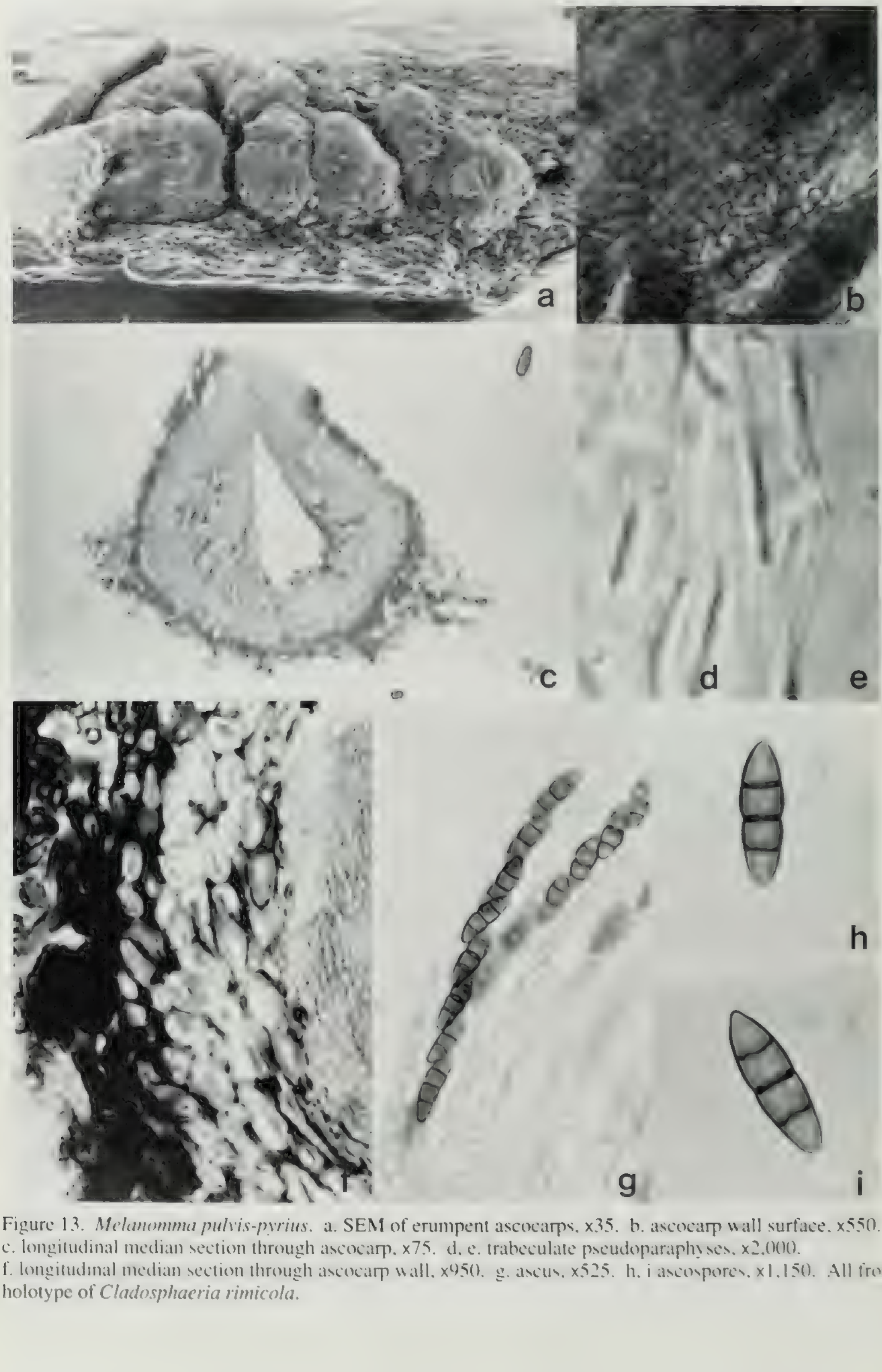

Figure 13. *Melanomma pulvis-pyrius*. a. SEM of erumpent ascocarps, x35. b. ascocarp wall surface, x550. c. longitudinal median section through ascocarp, x75. d, e. trabeculate pseudoparaphyses, x2,000. f. longitudinal median section through ascocarp wall, x950. g. ascus, x525. h, i ascospores, x1,150. All from holotype of *Cladosphaeria rimicola*.

Other material examined: SWITZERLAND: Bremengartenwald, on Prunus avium L. (holotype of *Cladosphaeria rimicola*, BERN). UNITED STATES: CALIFORNIA: Spruce Cove Heads, Trinidad, Humbolt Co., on *Rubus parviflorus*, 30 Jan. 1941, H.E. Parks 6513 (FH).

Comments: *Leptosphaeria rimicola*, described from the fallen branches of *Prunus avium* L., is synonymous with *Melanomma pulvis-pyrius*. *Leptosphaeria rimicola* has the overall appearance of *M. pulvis-pyrius*, with large, gregarious, superficial ascocarps and ascospores with the characteristic *Melanomma* shape: 3-septate with the primary median septum dividing the spore into a wider anterior and a narrower posterior part. The measurements of the ascospores of *L. rimicola* are somewhat larger than were found by Chesters (1938) for *M. pulvis-pyrius*, but they are not beyond the range for *M. pulvis-pyrius* given by Saccardo (1878). The asci peripherally lining the centrum about halfway up the wall and the ascocarp wall composed of small thickened cells correspond to Barr's (1987a) concept of the genus *Melanomma*. The pseudoparaphyses are thin and flexuous, but the branchings and anastomoses are infrequent and the septa often show thickenings, making them difficult to accurately identify as trabeculate.

Leptosphaeria Species Referable to the Dothideales

The species in this chapter all belong in the Dothideales (*sensu* Barr 1987a). Barr's concept of this order differs considerably from the all-inclusive concept of von Arx and Müller (1975) or the broad concept of Eriksson and Hawksworth (1985, 1986). The Dothideales (Barr 1987a) are characterized by ascocarps without a hamathecium (although interthecial cells are often present) and by asci that tend to be ovoid to saccate, arranged in a basal fascicle or a basal layer. The families represented are the Dothioraceae and the Pseudosphaeriaceae.

Dothioraceae

•*Saccothecium sepincola* (E.M. Fries:E.M. Fries) E.M. Fries, Summa Vegetabilium Scandinaviae, p. 398. 1849. See Figure 14.

≡ *Sphaeria sepincola* E.M. Fries, Observationes Mycologicae. 1:181. 1815; Systema Mycologicum Sistens Fungorum 2:498. 1823. [As *saepincola*.]

≡ *Metasphaeria sepincola* (E.M. Fries: E.M. Fries) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:164. 1883. [As Fr? Fuckel.]

≡ *Leptosphaeria sepincola* (E.M. Fries:E.M. Fries) H.G. Winter, Dr. L. Rabenhorst's Kryptogaman-Flora von Deutschland, Oesterreich und der Schweiz, Second edition, 1(2):473. 1885.

≡ *Sphaerulina sepincola* (E.M. Fries: E.M. Fries) K. Starbäck, Botaniska Notiser 1890:117. 1890; Botanisches Zentralblatt, 46:261. 1891.

≡ *Pringsheimia sepincola* (E.M. Fries: E.M. Fries) F. v. Höhnel, Annales Mycologici 18:97. 1920.

≡ *Pleosphaerulina sepincola* (E.M. Fries: E.M. Fries) H. Rehm *in* F. v. Höhnel. Annales Mycologici 18:96. 1920.

≡ *Sclerodothis sepincola* (E.M. Fries: E.M. Fries) F. Petrak, Annales Mycologici 19:41. 1921.

For other synonyms see Barr (1972).

Ascocarps thickly scattered, immersed-subepidermal, globose, glabrous, 180–200 µm diameter, 170–180 µm high. **Ascocarp wall** of textura angularis in surface view; in longitudinal section 25–36 µm thick at sides and base, up to 45 µm thick at apex, composed of 7–8 layers of pseudoparenchymatic, polygonal cells (5–6 x 6–12 µm), outer 2–3 layers of isodiametric-to-elongate, brown-melanized cells, inner 4–5 layers of hyaline-subhyaline, thin-walled, elongate-compressed cells, at the base giving rise to a central column (18–23 µm high, 27–36 µm wide) of hyaline, isodiametric cells (3–4 µm diameter, but cell boundaries becoming obscured in mass) on which the asci are borne. **Papilla** broadly rounded, bluntly conical, 45–55 µm high, 55–70 µm wide. **Asci** 40–60 x (13–)15–25 µm, numerous, fasciculate, borne on a basal column, oblong-ovate to clavate, thick-walled, short-stalked, apex rounded and thickened, with 8 bi- to triseriate ascospores. **Ascospores** (17–)18.5–20.5(–22.5) x 5.0–7.2 µm, obovate, with acute end cells, broad above and tapering to a narrower base, straight to slightly curved; 4-5(-6)-septate, septa unevenly distributed, septation order 3:2:1:2:4 or 4:2:1:3:5, primary septum submedian, vertical septum occasionally present in second or third cell from the top; hyaline, wall smooth, without sheath or appendages.

Lectotype: Sweden: Ad ramos emortuos Rosae aliorumque fruticum (UPS).

Exsiccatae: Austria: Nassau, on *Rosa canina*, as *Metasphaeria sepincola*, 1894, Fuckel, Herbier Barbey-Boissier 385 (FH); Nassau, on *Rubus fruticosus*, as *Sphaerulina intermixta* (Berk & Br) Sacc, 1894, Fuckel, Herbier

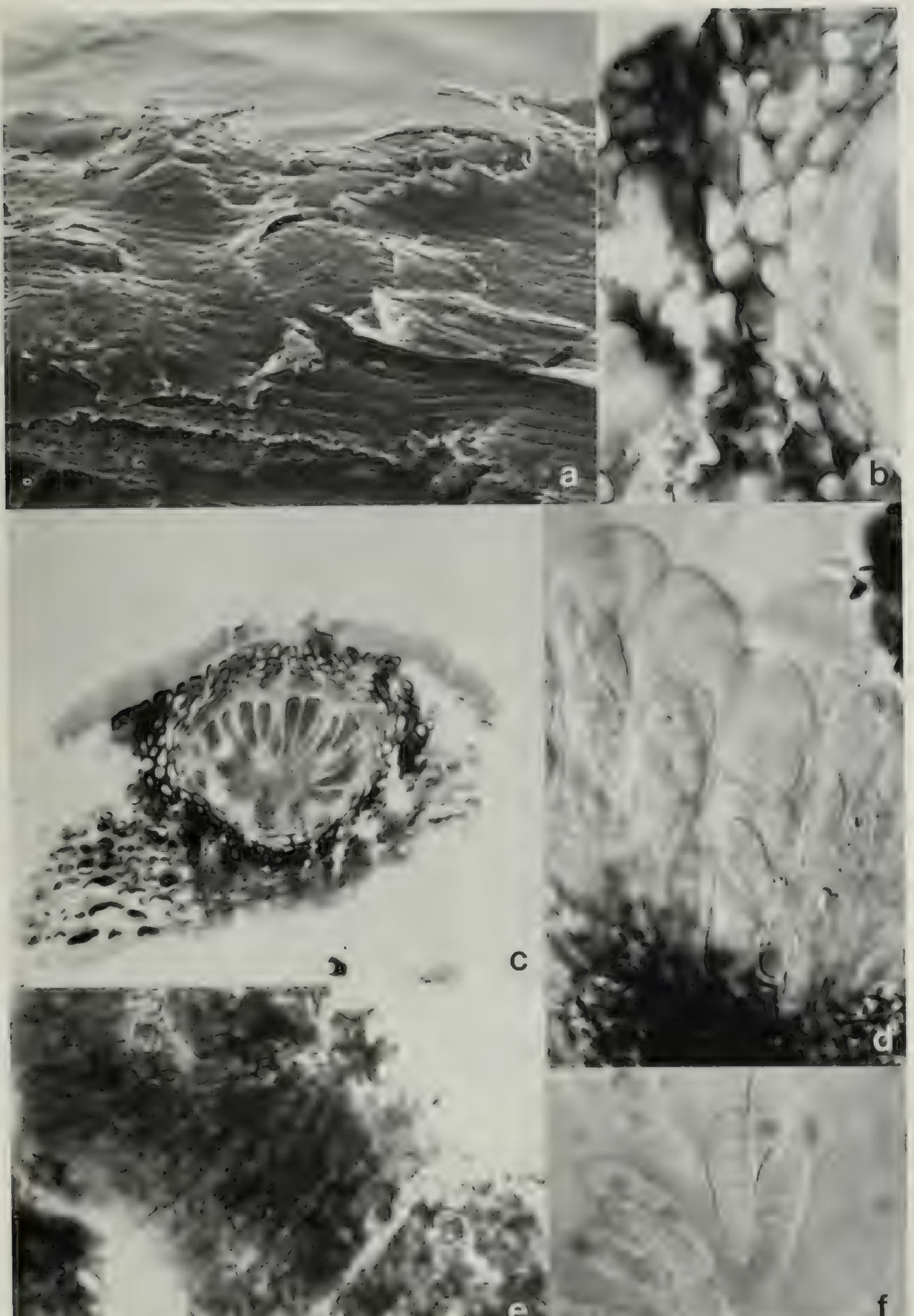

Figure 14. *Saccothecium sepincola*. a. SEM of immersed ascocarps, x125. b. longitudinal median section through ascocarp wall, x950. c. longitudinal median section through ascocarp, x225. d. asci, x1,050. e. ascocarp wall surface, x550. f. ascospores, x1,150. All from lectotype of *S. sepincola*.

rbey-Boissier 501 (FH); CZECHOSLOVAKIA: Weisskirchen, Ohrensdorf, as *Sphaerulina intermixta*, 25 Jan. 1912, Petrak, Fl. Boh. et Mor. exsic. Lfg. 4 Nr. 174. (FH); GERMANY: Leihterfeld bei Berlin, on *Philadelphus* sp., 1890, Sydow, Myc. March. 2934 (FH); ITALY: Selva, as *Sphaerulina intermixta*, Sept. 1878, Saccardo, Myc. Ven. 1367 (FH).

•*Saccothecium sepincola* var. *abbreviata* (M.C. Cooke) S.M. Huhndorf comb. nov. See Figure 15.

≡ *Sphaeria abbreviata* M.C. Cooke, Handbook of British Fungi, p. 893. 1871. (Basionym).

≡ *Leptosphaeria abbreviata* (M.C. Cooke) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:26. 1883.

Ascocarps 117–144 µm diameter, 81–99 µm high; wall 14–21 µm thick at the sides and apex, up to 27 µm thick at the base, composed of 7–8 layers of pseudoparenchymatic, polygonal cells (5–6 x 6–12 µm). **Papilla** broadly rounded. **Asci** (32–)41–61 x (13–)16.5–24.5 µm. **Ascospores** (12–)13.7–16.6 x 3.6–5.7 µm, 4-5(-6)-septate.

Holotype: GREAT BRITAIN: On dead stems of bramble. Jan.–April (K).

Comments: *Saccothecium sepincola* is not uncommon, but it has been confused by mycologists over the years as exemplified by the number of name changes based on the fungus. Wehmeyer (1957) gave an account of the history and nomenclatural confusion surrounding this species, including its relationships with other organisms and its relationship to the later genus *Pringsheimia* Schulzer von Müggenburg. He also included a lectotypification of *Saccothecium* Fr. Barr (1972) lists the taxonomic synonyms of *Saccothecium sepincola*. In some treatments, *Pringsheimia sepincola* is still used as the name for this species (Froidevaux 1973, von Arx and Müller 1975, Sivanesan 1984). Holm (1975) argued for the lectotypification of *Saccothecium* Fr. 1835 by *S. sepincola* (Fr.) Fr. 1849, which, as mentioned above, apparently was already done by Wehmeyer (1957) (see Dennis 1978). Holm (1975) does not mention the lectotypification by Wehmeyer, so it is unknown if this lectotypification was not accepted or if Holm overlooked Wehmeyer's work. In any case, with lectotypification, *Saccothecium* is the correct name and *Pringsheimia* becomes a synonym.

Saccothecium sepincola is placed in the family Dothioraceae by Barr (1987a) and is characterized by sphaeroid ascomata with walls of pseudoparenchymatous cells and oblong to clavate asci with a thickened apex which arise from a central basal column or mound of hypothecial cells. The septate, hyaline, obovate ascospores usually have a vertical septum present in one or more of the central cells. These characters suggest a similarity to some *Dothiora* species with raised basal areas (Barr 1972).

Leptosphaeria abbreviata is regarded as a variety of *Saccothecium sepincola* because ascospore sizes differ. The ascospores of *S. sepincola* are 17–22 x 5–7 µm, whereas the spores of *S. sepincola* var. *abbreviata* are 12–16 x 3–6 µm. The ascospores appear to be mature in specimens of both species. The ascocarps also differ in size between the two species in the specimens seen.

Some discrepancy exists between Cooke's (1871) description of *Sphaeria abbreviata* and the fungus that was present on the type specimen. Cooke's (1871) description includes "perithecia minute, in short parallel lines" and "asci very short and broad, elliptical, pyriform or obovate," which matches the fungus in the type. But then he describes spores that are "triseptate, slightly torulose and pale brown," which does not match this fungus, although occasionally the spores when mature may appear slightly pale brown. It is unclear whether his description was simply inaccurate or whether he was looking at two different fungi. Only one fungus is present on the type specimen and it was similar to *S. sepincola*.

Pseudosphaeriaceae

•*Leptosphaerulina pulchra* (H.G. Winter) M.E. Barr, Contributions de l'Institut Botanique de L'Université de Montréal 73:7. 1959. See Figure 16.

≡ *Sphaerella pulchra* H.G. Winter, Hedwigia 11:145–146. 1872.

≡ *Leptosphaeria pulchra* (H.G. Winter) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:53–54. 1883.

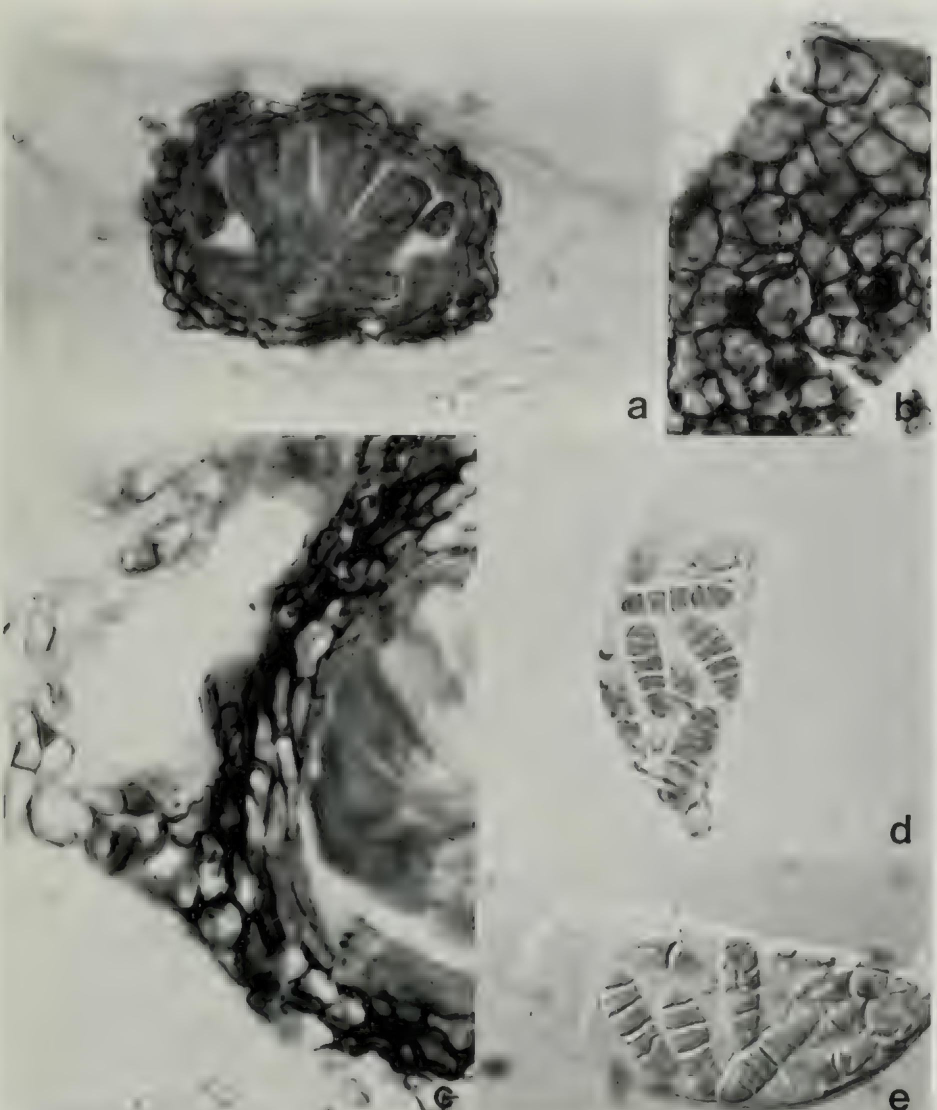

Figure 15. *Saccothecium sepincola* var. *abbreviata*. a. longitudinal median section through ascocarp, x375. b. ascocarp wall surface, x550. c. longitudinal median section through ascocarp wall, x950. d. ascus, x1,050. e. ascospores within an ascus, x1,150. All from holotype of *S. sepincola* var. *abbreviata*.

≡ *Mycotodea pulchra* (H.G. Winter) W. Kirschstein, Annales Mycologici 34:201. 1936; Kryptogamenflora de Mark Brandenburg und Angrenzender Gebiete herausgegeben von den Botanischen Verein der Provinz Brandenburg 7(3):433. 1938.

= *Leptosphaeria oligotheca* F. Petrak & H. Sydow, Annales Mycologici 22:359. 1924. [Described from type material of *Laestadia potentillae* E. Rostrup, Botanisk Tidsskrift 25:300. 1903.]

For other synonyms see Barr (1959).

Ascocarps thickly scattered, immersed-subcuticular, globose, papillate, glabrous, 50–75 µm diameter, 55–75 µm high. **Ascocarp wall** of textura globulosa in surface view; in longitudinal section uniformly 7.2–10.8(–12.7) µm thick, composed of 2–3 layers of pseudoparenchymatic, polygonal cells, outer 1–2 layers of brown-melanized cells (3.6–5.6 x 5.6–10.1 µm) covered by a brown-pigmented crust, inner 1–2 layers of hyaline, elongate-compressed cells (2.1–3.6 x 8.6–10.1 µm). **Papilla** short, erumpent, bluntly conical, 10–20 µm high, 10–21 µm wide at apex, 21–29 µm

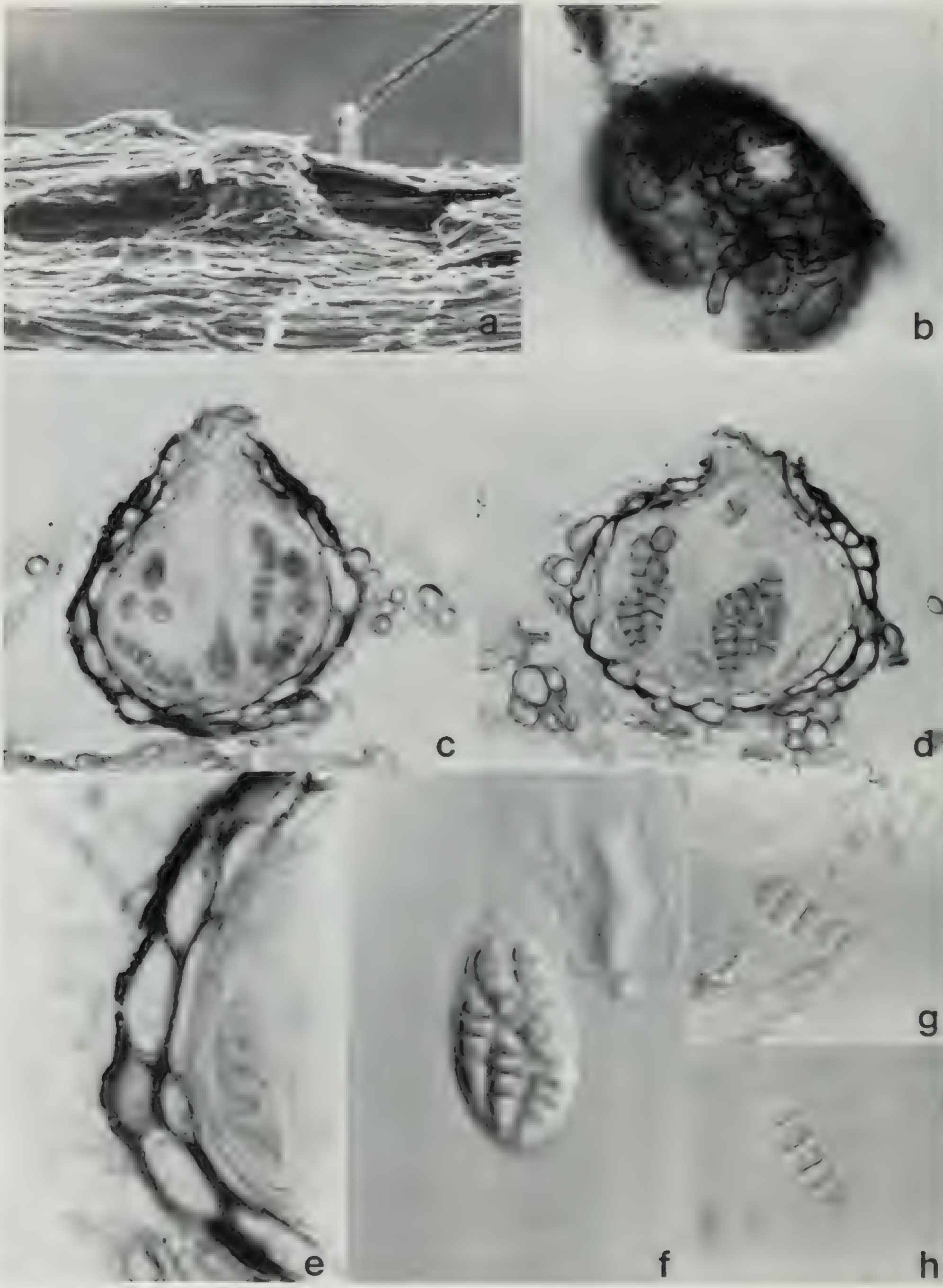

Figure 16. *Leptosphaerulina pulchra*. a. SEM of ascocarp, x250. b. ascocarp wall surface, x550. c, d. longitudinal median section through ascocarps, x650. e. longitudinal median sections through ascocarp wall, x950. f. ascus, x1,050. g, h. ascospores, x1,150. a, b, d, and f from holotype of *Leptosphaeria oligotheca*; c, e, g, and h from neotype of *Leptosphaerulina pulchra*.

wide at base, neck wall 3.6–8.6 µm thick, composed of 2–3 layers of isodiametric-elongate cells (3.6–4.3 x 3.6–6.5 µm) surrounding a circular ostiole (9–12 µm wide) without periphyses. Remnants of interthecial tissue remain between and above the asci. **Asci** 32–45 x 15–20 µm, few, basal, fasciculate, ovoid-saccate, thick-walled, sessile, rounded apex, without apical chamber, with 8 tri- to tetraseriate ascospores. **Ascospores** 17.2–20.8 x 5.7–7.2 µm, clavate to obovoid, bipolarly asymmetrical with broadly rounded apical end cell and acutely rounded basal end cell, straight; 4(-5)-septate, septa unevenly distributed, order of septation 3:1:2:4, primary septum supramedian and constricted, a single vertical septum occasionally present in the central cells; subhyaline to pale brownish yellow, wall smooth, without sheath or appendages.

Holotype: Austria: Ad caules foliaque aridos *Potentillae caulescentis*, "am Martinstein bei Seis in Tyrol" 1870 von v. Hausmann gesammelt (B), (n.v.), presumed destroyed.

Neotype: United States: Maine: Basin Pond, Baxter St. Park, July 5, 1962, MEBB # 3316 (NY).

Other material examined: Canada: Labrador, Newfoundland, Blanc Sablon, July 19, 1957, R.T. Wilce #161 (NY). Iceland: on *Potentilla maculata*, type material of *Laestadia potentillae* Rostrup, July 14, 1884 (Holotype of *Leptosphaeria oligotheca*, C). United States: Maine: Mt. Katahdin, Baxter St. Park, Tablelands from Saddle Trail, ca. 4200', Aug. 3, 1962, MEBB # 3546 (NY); New Hampshire: Mt. Washington, on *Potentilla tridentata*, June 9, 1894 (FH as *Sphaerulina potentillae*); Mt. Monadnock, near Dublin, June 27, 1961, MEBB # 2927 (NY).

Comments: *Leptosphaerulina pulchra* is placed in the family Pseudosphaeriaceae because of the minute, sphaeroid-globose ascocarps with a very thin wall composed of pseudoparenchymatous cells and the interthecial tissues. The species is recognized readily on the basis of its saccate asci, ascospore shape, and septation. Barr (1959) mentions the presence of a vertical septum in the central cells, but in most of the collections seen, vertical septa were lacking. Still, the obovate, asymmetrical ascospore shape is distinctive.

The holotype of *Leptosphaerulina pulchra* at B, not located, is presumed to have been destroyed with the rest of the ascomycete collection during World War II. Also unsuccessful were attempts to locate authentic material of Winter or of the collector, von Hausmann. Because of this, a neotype for *L. pulchra* was chosen (Maine: Basin Pond, Baxter St. Park, July 5, 1962, MEBB # 3316) from the M.E. Barr collection now at NY. The neotype reflects both the original description and the current, well-established concept of this species.

Leptosphaeria oligotheca is synonymous with *Leptosphaerulina pulchra*. When Petrak and Sydow (1924) originally described *Leptosphaeria oligotheca* from material on the type of *Laestadia potentillae*, on stems of *Potentilla maculata*, they did not segregate any of the material as the holotype for *L. oligotheca* and none could be found with their herbarium specimens at W or S. The type specimen of *Laestadia potentillae* at C contained abundant material matching the description of *Leptosphaeria oligotheca*, so a portion was segregated as the holotype of that fungus.

Barr (1959) mentions several other species whose descriptions suggest they may be synonymous with *Leptosphaerulina pulchra*. One of these was *Sphaeria minima* Duby *in* C. Roumeguère, Fungi Selecti Gallici Exsiccati, Century 7, No. 694. Anno 1880. Examining specimens from the exsiccatae sets at G, FH, NY, and ILL showed that they included many ascocarps, but none contained asci or ascospores. Therefore, it was impossible to resolve the placement of this species.

•*Diadema obtusa* R.A. Shoemaker & C.E. Babcock, Canadian Journal of Botany 67: 1353–1354. 1989. See Figure 17.

Ascocarps thickly scattered, immersed-subcuticular becoming erumpent, globose, glabrous to slightly tomentose, with smooth brown hairs, 100–150 µm diameter, 120–150 µm high. **Ascocarp wall** of textura angularis in surface view; in longitudinal section (7.5–) 10–18 µm thick at sides and base, composed of 2–3 layers of brown-melanized, polygonal, pseudoparenchymatic cells (1.8–4.3 x 7–11

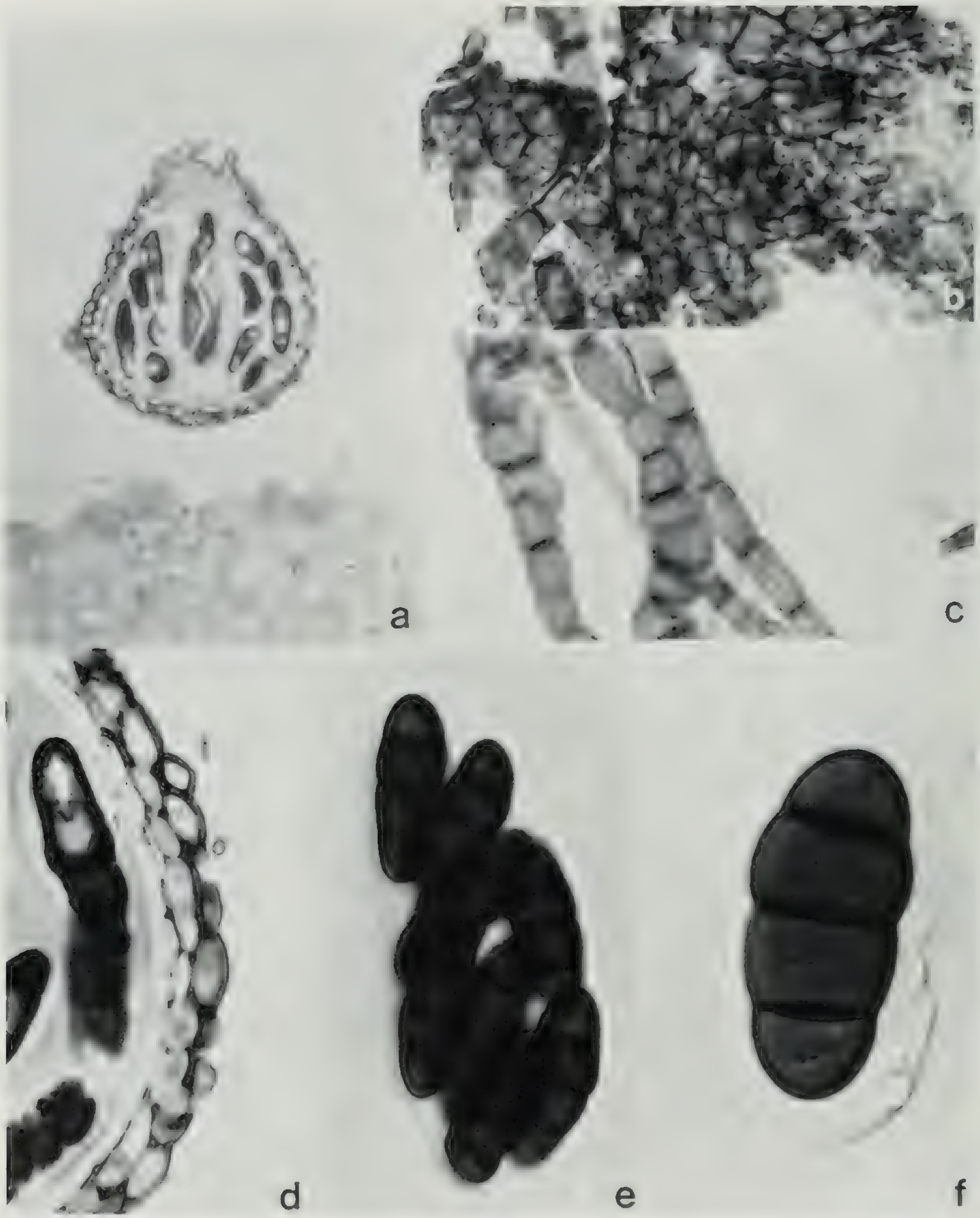

Figure 17. *Diadema obtusa*. a. longitudinal median section through ascocarp, x250. b. ascocarp wall surface, x550. c. hyphae on substrate surface, x550. d. longitudinal median section through ascocarp wall, x950. e. ascus, x525. f. ascospore, x1,050. All from collection 123871, on *Potentilla agrophylla*.

μm). **Apex** broadly rounded, 18–27 μm thick, 45–65 μm diameter, composed of 2–3 outer layers of brown-melanized, isodiametric cells (3.6–5.4 μm diameter) with 6–8 layers of hyaline pseudoparenchyma below center, opening area not seen, possibly discoid, caplike opening lacking, ostiole not seen. Interthecial tissues present. **Asci** (100–)120–145 x (30–) 50–70 μm, few, basal, fasciculate, ovoid-saccate to clavate, thick-walled, short-stalked, rounded apex, with apical chamber, with 8 tri- to tetraseriate ascospores. **Ascospores** (41.5–) 45–50(–55) x (15–17–)19–23 μm, broadly fusiform, acutely rounded end cells, second cell

enlarged, straight to slightly curved, occasionally flattened in one plane; 3-septate, septa slightly unevenly distributed, order of septation 2:1:2, primary septum median and constricted, slightly constricted at other septa; brown, wall smooth, sharply delimited sheath entirely surrounding spore (5–7.5 µm thick), without appendages.

Holotype: INDIA: KASHMIR: 123831(b), on *Trisetum spicatum*, Pensi La, Zaskar, 16,500 ft. W. Koelz (5906), 23 July 1933, TYPE, ex Herb. Wehmeyer, as *Leptosphaeria hollosiana* nom. nov. (DAOM).

Other material examined: INDIA: 123871, on *Potentilla agrophylla* Wall., Spiti Valley, Bara Lacha Pass, 16,500 ft, Bhagwan Singh (5), 8 July 1932, ex Herb. Wehmeyer, as *Leptosphaeria hollosiana* nom. nov. (DAOM).

Comments: Shoemaker and Babcock (1989a) established the new genus *Diadema* for a group of alpine fungi with relatively large, very dark brown ascospores. They did not place the genus within a family or order. Eriksson and Hawksworth (1990) placed it in the Dothideales but did not designate a family. In the present report I treat it under the Pseudosphaeriaceae because it resembles *Wettsteinina* Höhnel; for example, some species have a peculiar disclike opening of the ascocarp and have interthecial tissue in the centrum. *Diadema* is characterized by globose, subcuticular ascocarps with a thin wall of brown polygonal cells and broadly fusiform ascospores that are dark brown and have a prominent sheath.

Wehmeyer (1963) published the name *Leptosphaeria hollosiana* for *Leptosphaeria maritima* L. Hollós because the latter binomial was predated by *L. maritima* (Cke. & Plowr.) Sacc. He applied the new name to several collections from India and Pakistan, including two collections on *Potentilla*. Shoemaker and Babcock (1989a) described two new species of *Diadema* from these collections, including the type of the genus, *D. acuta*, on *Trisetum spicatum* (L.) Richt., and *D. obtusa*, also on that host. The collections on *Potentilla* were also determined to be *D. obtusa*. The collection on *Potentilla* served as the basis for this description and plate because of the Rosaceous host and because it had numerous ascocarps. The other collections of *D. obtusa* were sparse.

As Shoemaker and Babcock (1989a) noted, the ascocarp opening mechanism in this species is not clearly understood. It is not distinctly caplike but in vertical section becomes almost papillate (Figure 17a). The entire upper section of the wall is subtended by hyaline pseudoparenchyma. Interthecial pseudoparenchymatic threads occurred between the asci. Also, coarse, brown hyphae were seen on the host surrounding several of the ascocarps, and some of the ascocarps were not glabrous but had tapered hairs at the top. I did not see the ascospores flattened in one plane, as did Shoemaker and Babcock (1989a). Shoemaker and Babcock (1989a) suggested that the generic placement of this species is not ideal because several characters were not identical to those of the type species. The overall aspect of this species, however, suggests an affinity with the type species, and that it is adequately placed in this genus. It appears that certain characters, such as the ascocarp cap and interthecial tissues, are variable among collections and may depend on the maturity of the specimen, as was also noted by Shoemaker and Babcock (1989a). Species of *Wettsteinina* are similarly variable, either showing a disclike cap or an ostiolar opening to the ascocarp; species with either character state are adequately retained within the genus because of overall resemblances (Shoemaker and Babcock 1987). Thus, such variation does not appear sufficient to exclude species from these genera.

•*Diadema sieversiae* (C.H. Peck) S.M. Huhndorf comb. nov. See Figure 18.

≡ *Lophiostoma sieversiae* C.H. Peck, New York State Museum Bulletin 167:44. 1913. (Basionym).

≡ *Wettsteinina sieversiae* (C.H. Peck) M.E. Barr, Canadian Journal of Botany 45:1042. 1967.

= *Massaria sieversiae* F.E. Clements, Cryptogamae Formationum Coloradensium, Century III, No. 234. Anno 1906. Nom. nud. Art. 36.1.

≡ *Leptosphaeria sieversiae* (F.E. Clements) F. Petrak, Sydowia. Annales Mycologici 6(1-4):6. 1952. [Combination is not valid because the basionym is an invalidly published species.]

Ascocarps thickly scattered, immersed-subcuticular becoming erumpent, globose,

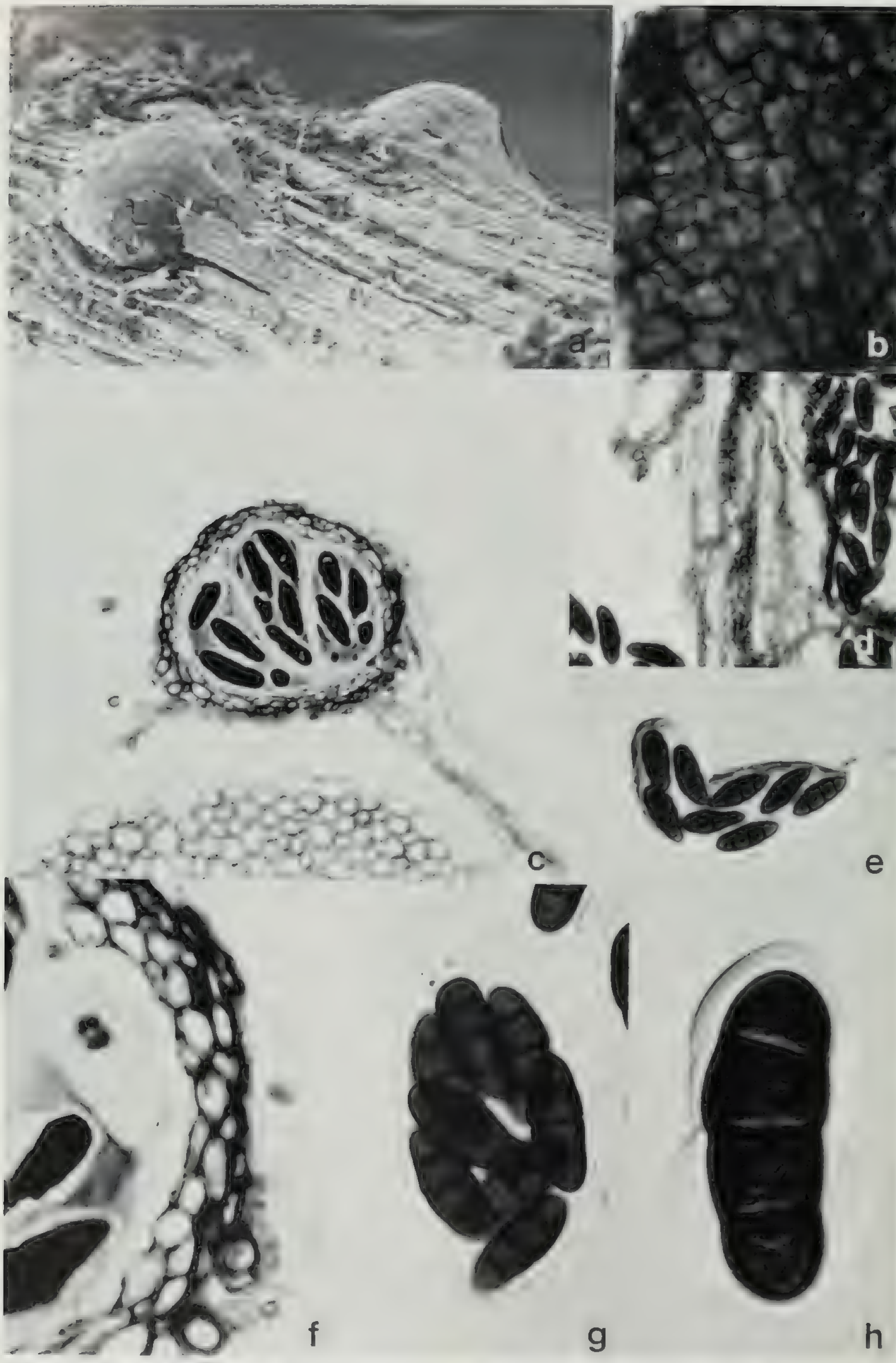

Figure 18. *Diadema sieversiae*. a. SEM of erumpent ascocarps, x125. b. ascocarp wall surface, x550. c. longitudinal median section through ascocarp, x250. d. hyphae on substrate surface, x200. e. elongated ascus, x250. f. longitudinal median section through ascocarp wall, x950. g. ascus, x525. h. ascospore, x1,050. a, b from holotype of *D. sieversiae*; c–h from isotype of *Massaria sieversiae*.

glabrous to slightly tomentose, with loose dark-walled, longitudinal hyphae on the substrate, surrounding and connecting the ascocarps, 130–190 µm diameter, 120–175 µm high. **Ascocarp wall** of textura angularis in surface view; in longitudinal section uniformly 12.6–20 µm thick, composed of 3–4 layers of brown-melanized, pseudoparenchymatic, polygonal, isodiametric-elongate cells (3.6–5.6 x 7.2–13 µm) with a brown-melanized crust, at base 3–4 inner layers of small, hyaline pseudoparenchyma. **Apex** broadly rounded, with inner 3–4 layers of hyaline, pseudoparenchymatic cells (2–5 µm diameter), no evidence of papillate or caplike opening, ostiole not seen. Interascal pseudoparenchyma present. **Asci** (110–)130–170 x 40–70 µm, few, basal, fasciculate, ovoid-saccate, thick-walled, sessile, rounded apex, with apical chamber, with 8 tri- to tetraseriate ascospores. **Ascospores** (43.5–)50.6–56.0 (–57.9) x (16–)20–23.5(–25.5) µm, broadly fusiform, with acutely rounded end cells, second cell enlarged, straight to slightly curved; 3-septate, septa slightly unevenly distributed, order of septation 2:1:2, primary septum slightly supramedian and constricted, occasionally constricted at other septa; brown, wall smooth, sharply delimited sheath entirely surrounding spore [2.0–5.5(–10.5) µm thick, often constricted at midseptum, sheath occasionally gelatinizing and becoming amorphous (7–12 µm thick)], without appendages.

Holotype: UNITED STATES: UTAH: 193727, on *Sieversia turbinata* (Rydb.) Greene, Big Cottonwood Canyon, Salt Lake Co., A.O. Garrett 702, 3 July 1913 (NYS).

Exsiccatae: UNITED STATES: COLORADO: Bottomless Pit, July 13, 1906, Clements, Crypt. Form. Colorad. 234 (isotype of *Massaria sieversiae*, NY, FH).

Comments: *Diadema sieversiae*, found on stems of *Acomastylis turbinata*, is characterized by globose ascocarps with thin walls of brown polygonal cells, dark-walled hyphae on the substrate, and broadly fusiform, dark brown ascospores with a prominant gelatinous sheath. It bears a strong resemblance to *D. obtusa*, but in that species the spores are slightly shorter and the dark brown hyphae in the host are not as prevalent. The ascocarp shapes differ somewhat, but I also saw no indication of a cap or disclike opening mechanism in *D. sieversiae*. Interthecial tissues were seen between the asci.

Diadema sieversiae was described by Peck (1913) as a species of *Lophiostoma*, but it bears no compressed beak or ostiole that would warrant inclusion in that genus. Barr (1967) transferred it to *Wettsteinina* because of the medium- to small-sized ascocarps immersed in dead host tissues and the oblong to saccate asci interspersed with interthecial tissue. Shoemaker and Babcock (1987) excluded it from *Wettsteinina* because of the dark brown ascospores with thick septa that are unlike the usual spores for *Wettsteinina*. It was left in *Lophiostoma* and later (Shoemaker and Babcock 1989a) was not included in *Diadema*. Clearly this fungus does not belong in *Lophiostoma*, and it bears a much greater resemblance to *Diadema* than to *Wettsteinina*. Even if it ultimately does not stay in *Diadema*, because of the lack of a disclike cap opening (as suggested for *D. obtusa* by Shoemaker and Babcock 1989a), it seems useful to place this species in *Diadema*, in the hope that additional collections may be discovered.

Massaria sieversiae, which was transferred to *Leptosphaeria*, is synonymous with *Diadema sieversiae*.

Leptosphaeria Species Referable to the Hymenoascomycetes

The following *Leptosphaeria* species are all referable to the class Hymenoascomycetes (*sensu* Barr 1987a). The presence of perithecia and unitunicate asci separates these fungi from those in the Loculoascomycetes possessing pseudothecia and bitunicate asci. The families represented are Clypeosphaeriaceae, Diaporthaceae, and Amphisphaeriaceae.

Clypeosphaeriaceae

•*Clypeosphaeria mamillana* (E.M. Fries:E.M. Fries) J.B.E. Lambotte, Memoires de la Societe Royale des Sciences de Liege, ser 2, 14:128. 1887. See Figure 19.

≡ *Sphaeria mamillana* E.M. Fries:E.M. Fries, Systema Mycologicum 2:487. 1823.

= *Sphaeria clypeiformis* G. de Notaris, Memorie della Accademie della Scienze di Torino Series 2, No. 7, p. 113. 1853; Micromycetes Italici Novi vel Minus Cogniti 7, p. 113. 1845. Non *Sphaeria clypeiformis* L.V. de Lacroix *in* G.L. Rabenhorst.

≡ *Clypeosphaeria notarisii* L. Fuckel, Symbolae Mycologicae, p. 117. 1870.

≡ *Leptosphaeria (Clypeosphaeria) notarisii* M.C. Cooke, Grevillea 17:91. 1889.

See Barr (1989) for other synonyms.

Ascocarps scattered, separate or gregarious, immersed-subepidermal beneath blackened clypei, papilla erumpent, glabrous, conic-globose, 300–400 µm diameter, 400–450 µm high. **Ascocarp wall** of textura angularis in surface view; in longitudinal section uniformly 18–25 µm thick, composed of 10–15 layers of hyaline, elongate-compressed, scleroplectenchymatic cells (0.7–1.5 x 7–15 µm), outer 2–3 layers of hyaline, rounded, polygonal cells (2.0–3.6 µm diameter). **Papilla** conic, 130–160 µm high, 50–75 µm wide at the apex, 150–225 µm wide at the base; wall 15–30 µm thick at apex, 35–65 µm thick at base, composed of 10–15 layers of small, brown-melanized, thick-walled, rounded, polygonal cells at base (1.5–3.6 µm diam), cells converging and appearing as elongate, setaelike structures at apex, surrounding a 25–50 µm wide circular ostiole with periphyses. **Paraphyses** 0.5–1.5 µm wide, numerous. **Asci** 150–170 x 8–10 µm, unitunicate, numerous, basal to peripheral, cylindrical, short-stalked, rounded apex, apical ring J+, with 8 overlapping uniseriate ascospores. **Ascospores** 21–26 x 5.7–8 µm, ovoid-oblong, straight to slightly curved; at times 1-septate near base, large cell appearing 3-septate with separation of cytoplasm; brown, smooth, without sheath or appendages, germ slits not seen.

Exsiccatae: Austria: On *Rubus fruticosus*, Fuckel, F. rhen. 1823 (FH); Mappen, on *Epilobium angustifolii*, as *Sordaria clypeiformis* f. *Epilobii*, Fuckel, F. rhen. 2036 (FH); Herb. Barbey-Boissier 146 = F. rhen. 1823, as *C. notarisii* (NY); Great Britain: Lynn, on *Epilobium hirsutum*, as *Sphaeria clypeata* Nees., Jan. 1877, Plowright, Sphaer. Brit. 57 (FH); Italy: on *Rubus fruticosus*, as *Sphaeria clypeiformis*, Aug. 1857, leg. Caldesi, Rabenhorst, Herb. myc. 645 (FH); as *Sphaeria clypeiformis*, 1857, leg. Caldesi, de Notaris, Erb. Critt. Ital. 47 (FH); La Spezia, as *C. notarisii*, Aug. 1880, Roumeguere, F. Gall. exs. 2095 (NY); Vittorio (Treviso), on *Rubus fruticosus*, as *C. notarisii*, Sept. 1897, Saccardo, Mycotheca ital. 101 (NY); Conegliano, as *C. notarisii*, Aug. 1877, Mycotheca veneta 1159 (NY); St. Romani-ad-Vigennam, as *S. clypeiformis* de Lcrx., 1859, leg. T. de Lacroix, Rabenhorst, F. europ. 331 (RO).

Other material examined: Italy: Capraria, on *Rubus*, as *Sphaeria sepincola ruborum*, 1837,

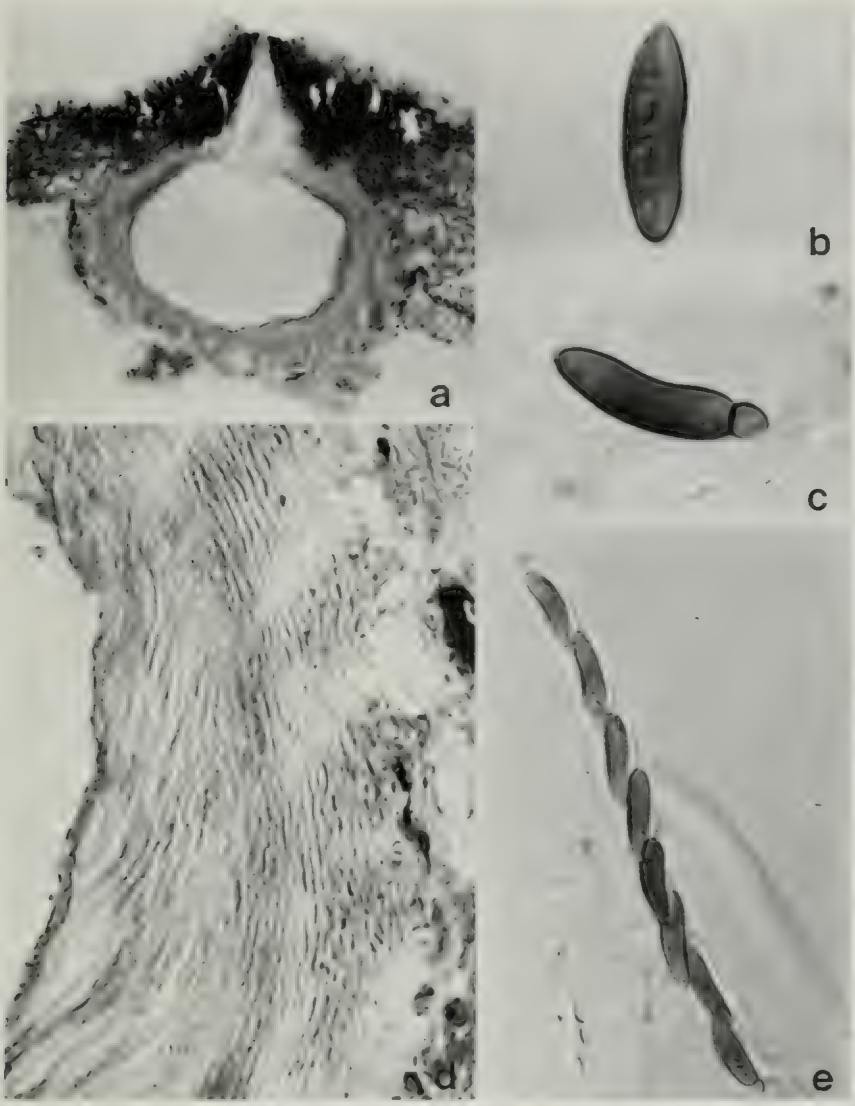

Figure 19. *Clypeosphaeria mamillana*. a. longitudinal median section through ascocarp, x100. b, c. ascospores, x1,150. d. longitudinal median section through ascocarp wall, x950. e. ascus, x525. All from lectotype of *C. notarisii*.

de Notaris (Lectotype of *Sphaeria clypeiformis*); two collections of *Sphaeria clypeata*, 1840; Spezia, Aug. 1857, Herb. N.A. Pedicino, 1883; on *Rubus*, as *S. clypeiformis*, Mar. 17, 1842, de Notaris (all RO).

Comments: *Clypeosphaeria notarisii*, a synonym of *Clypeosphaeria mamillana*, is characterized by cylindrical asci with an elongate, J+ apical ring and curved, brown ascospores appearing 3-septate with separation of the cytoplasm. Barr (1989) gives the synonymy and a short history of *Clypeosphaeria* and argues for the utilization of the family Clypeosphaeriaceae.

Clypeosphaeria was established by Fuckel (1870), who included *C. notarisii* as a new name for *Sphaeria clypeiformis* de Not. A specimen of *Sphaeria sepincola ruborum* was mentioned in the description of *Sphaeria clypeiformis*, and a collection of this at RO is here designated as the lectotype of *S. clypeiformis* (ITALY: Capraria, on *Rubus*, 1837, de Notaris, RO).

Diaporthaceae

•*Diaporthe eres* T.R.J. Nitschke, Pyrenomycetes germanici, p. 245. 1867. See Figure 20.
= *Sphaeria controversa* J. Desmazierès (pro parte), Annales des Sciences Naturelles, Paris, Botanique, Series 2, 17:102. 1842.
≡ *Leptosphaeria controversa* (J. Desmazierès) V. Cesati & G. de Notaris, Commentario della Societa Crittogamologica Italiana 1:235. 1863.
≡ *Diaporthe controversa* (J. Desmazierès) T.R.J. Nitschke *in* L. Fuckel, Symbolae Mycologicae Nachtrag 1:319. 1871.
See Wehmeyer (1933) for other synonyms.

Ascocarps scattered, separate or clustered, immersed-subepidermal often beneath blackened stromatic tissue, papilla erumpent singly or in loose clusters, glabrous, globose, flattened at top and base, 300–400 µm diameter, 250–350 µm high. **Ascocarp wall** of textura angularis in surface view; in longitudinal section 25–35 µm thick at the sides, 15–20 µm thick at the base, composed of 7–8 layers of hyaline, elongate-compressed, scleroplectenchymatic cells (0.7–1.5 x 10–15 µm), wall near apex 45–50 µm thick, composed of 10–12 layers of brown-melanized, polygonal, isodiametric cells (2–3 µm diam). **Papilla** long cylindrical, central or eccentric, 125–180 µm high, 50–75 µm wide; wall 25–35 µm thick, composed of small, brown-melanized, thick-walled, rounded, polygonal cells (1.5–3.0 µm diameter), surrounding a 25–40 µm wide circular ostiole with periphyses. **Paraphyses** 0.5–1.5 µm wide, numerous, septate, unbranched. **Asci** 38–55 x 6–8.5 µm, unitunicate, numerous, basal to peripheral, dehiscent, clavate, short-stalked, rounded apex, with 8 biseriate ascospores. **Ascospores** 10.5–13.5 x 2.0–3.6 µm, fusiform, straight to slightly curved; 1-septate, constricted; hyaline, with four distinct oil droplets, smooth, without sheath, occasionally with small, cellular bipolar appendages.

Isotype: FRANCE: Habitat in caulibus plantarum, in ramis exsiccatis Fraxini, Rubi, Aceris Negundinis, etc. Desm. Pl. Crypt. Fr. exs. XXVI 1255 (PC, FH, BPI).

Comments: *Sphaeria controversa* (pro parte) is synonymous with *Diaporthe eres* (Wehmeyer 1933) and is characterized by ascocarps immersed beneath blackened stromata, with central or eccentric, long cylindrical necks with periphyses. As they mature, the numerous asci loosen and become free within the centrum. Ascospores are hyaline and 1-septate and have four distinct oil droplets.

The exsiccati collections all consisted of several different twigs of unknown identity, none of which appeared to be *Rubus*, most with varying amounts of the fungus on them.

Amphisphaeriaceae

•*Discostroma fuscella* (M.J. Berkeley & C.E. Broome) S.M. Huhndorf comb. nov. See Figure 21.
≡ *Sphaeria (Obtectae) fuscella* M.J. Berkeley & C.E. Broome, Annals and Magazine of Natural History, London, Series 2, 9:325. 1852. (Basionym).
≡ *Leptosphaeria fuscella* (M.J. Berkeley & C.E. Broome) V. Cesati & G. de Notaris, Commentario della Società Crittogamologica Italiana 1:236. 1863.
= *Sphaeria corticola* L. Fuckel, Symbolae Mycologicae, p. 114, 1870.
≡ *Leptosphaeria corticola* (L. Fuckel) P.A. Saccardo, Michelia Commentarium Mycologicum Fungos in Primis Italicos Illustrans 1:342. 1878; Fungi Italici autographice delineati (additis nonnullis extra-italicis asterisco notatis), Patavii, table 288. 1878.
≡ *Metasphaeria corticola* (L. Fuckel) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:166. 1883.
≡ *Griphosphaeria corticola* (L. Fuckel) F. v. Höhnel, Annales Mycologici 16:87. 1918.
≡ *Clathridium corticola* (L. Fuckel) R.A. Shoemaker & E. Müller, Canadian Journal of Botany 42:404. 1964.
≡ *Discostroma corticola* (L. Fuckel) I. Brockmann, Sydowia 28:313. 1975.
= *Sphaeria (Leptosphaeria) leiostega* J.B. Ellis, Bulletin of the Torrey Botanical Club (and Torreya) 8:91. 1881.
≡ *Leptosphaeria leiostega* (J.B. Ellis) J.B. Ellis, Catalogue of Plants Found in New Jersey, Geological Survey of New Jersey, Final Report of the State Geologist 2(1):525. 1889.

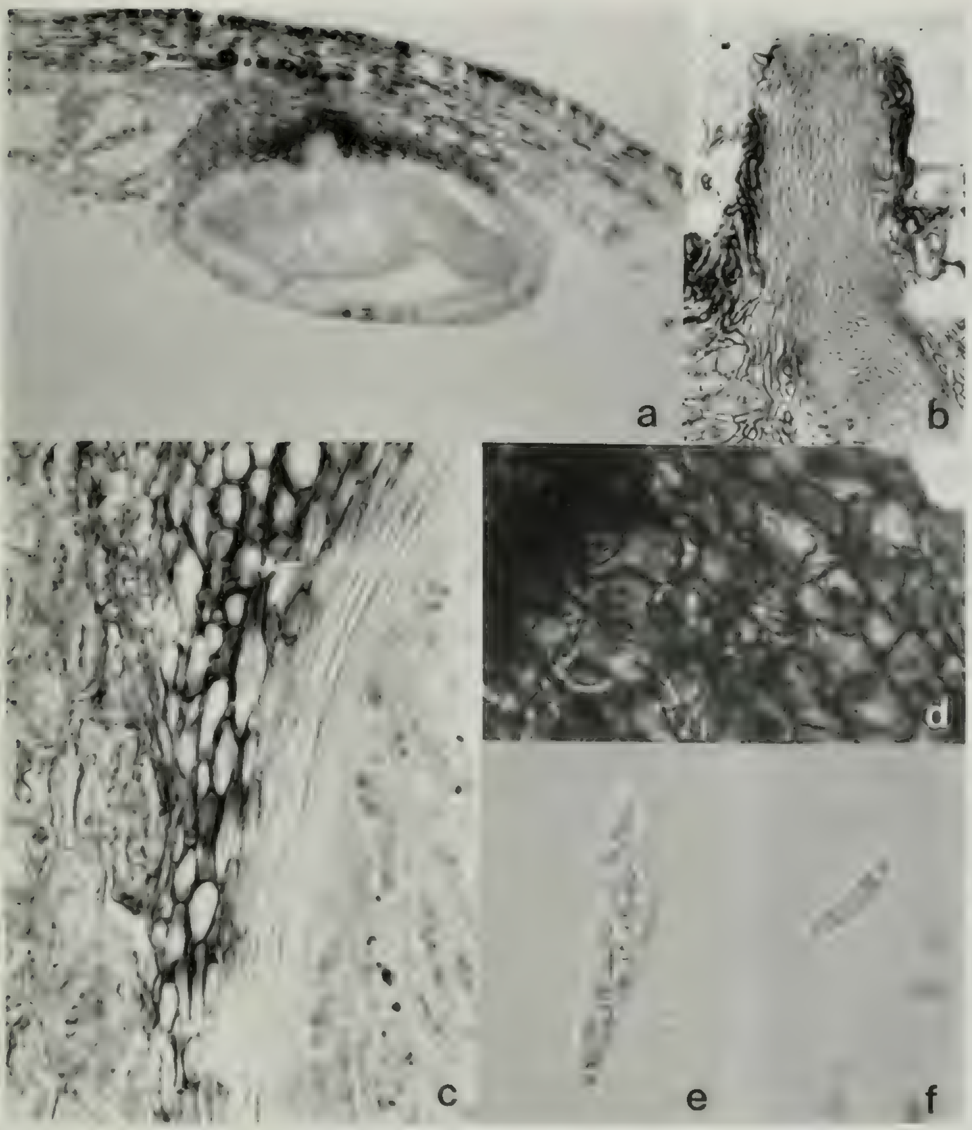

Figure 20. *Diaporthe eres*. a. longitudinal median section through ascocarp, x150. b. section through ascocarp neck showing periphyses, x400. c. longitudinal median section through ascocarp wall, x950. d. ascocarp wall surface, x550. e. ascus, x1,050. f. ascospore, x1,150. All from type of *Leptosphaeria controversa*.

≡ *Leptosphaeria lejostega* (J.B. Ellis) F. Hazslinszky, Matematikai és Természettudományi Közlemenyek Vonatkozólag a Hazai Viszonyokra 25(2):148. 1892.

≡ *Metasphaeria lejostega* (J.B. Ellis) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:164. 1883.

For other synonyms see Brockmann (1975).

Ascocarps scattered, separate or clustered, immersed-subepidermal beneath blackened clypei, glabrous, depressed globose, flattened top and bottom, with papilla protruding through surface, 300–500 µm diameter, 150–250 µm high. **Ascocarp wall** of textura prismatica in surface view; in longitudinal section 8–18 µm thick at base, 18–27 µm thick at sides, composed of 6–8 layers of brown, elongate-compressed, scleroplectenchymatic cells (12–

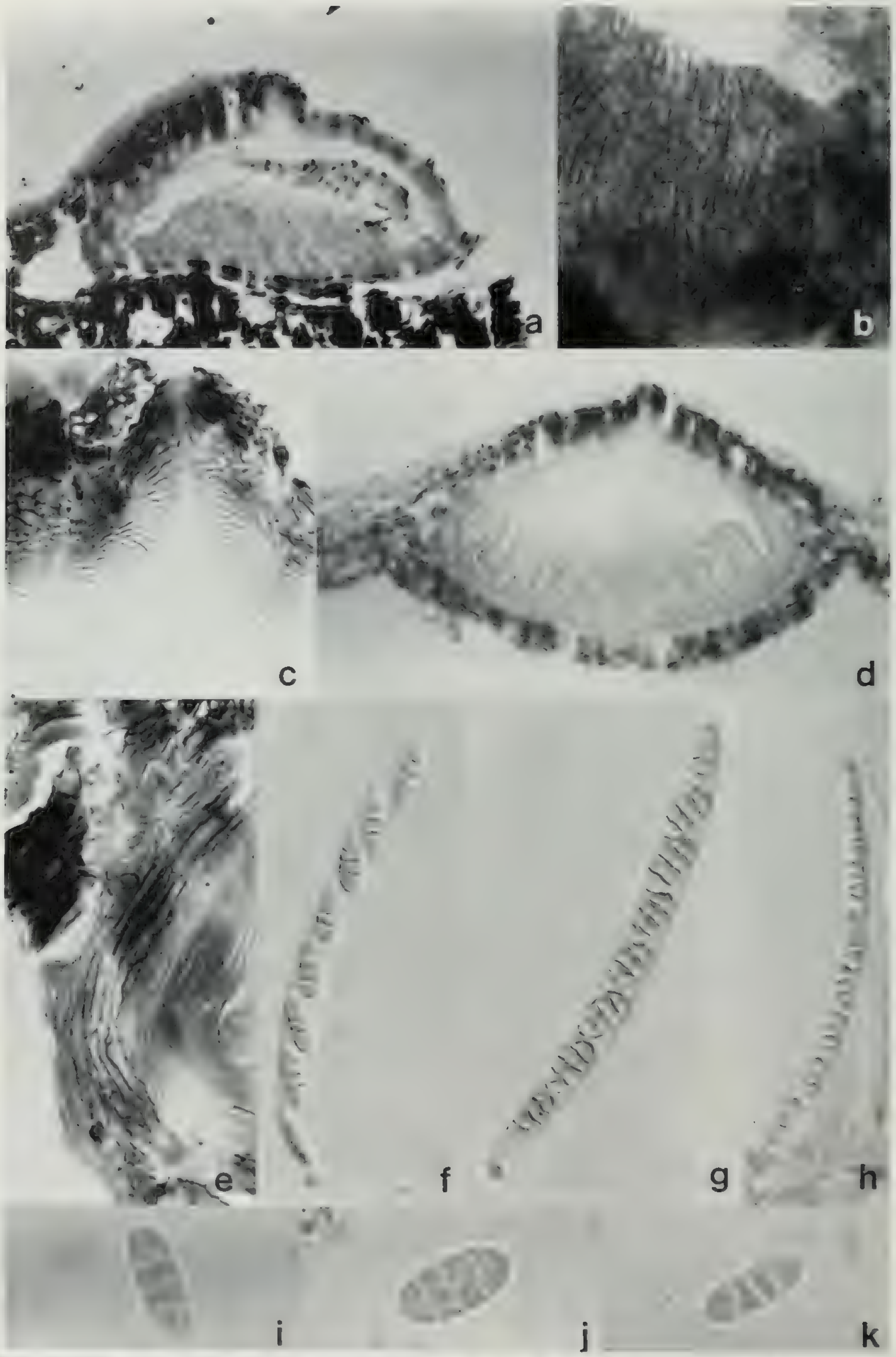

Figure 21. *Discostroma fuscella*. a. longitudinal median section through ascocarp, x150. b. ascocarp wall urface, x550. c. section through ascocarp wall neck region, x550. d. longitudinal median section through rp, x150. e. longitudinal median section through ascocarp wall, x950. f–h. asci, x525. i–k. ascospores. c, e, f, and i from holotype of *D. fuscella*; d, g, and j from lectotype of *Sphaeria leiostega*; pe of *S. corticola*.

25 x 2–3 µm); near apex, wall 21–36 µm thick, composed of 6–7 outer layers of brown, polygonal-isodiametric cells (7–11.5 x 2–3; 2.1–3.6 µm diameter) and 6–7 inner layers of compressed-elongate, scleroplectenchymatic cells. **Papilla** conical, 50–75 µm high, 20–30 µm wide at the apex, 35–50 µm wide at the base; wall 7–10 µm thick, composed of 7–10 layers of small, brown-melanized, thick-walled, rounded, polygonal cells, surrounding a 10–20 µm wide circular ostiole with periphyses. **Paraphyses** 0.5–1.5 µm wide, numerous, septate, unbranched. **Asci** (101–)115–132 (–137) x 7–12(–14) µm, unitunicate, numerous, basal in a broad hymenium, cylindrical, short-stalked, rounded apex, apical ring J+, with 8 overlapping uniseriate ascospores. **Ascospores** 15–21 x 5–9.5 µm, ellipsoidal, end cells rounded; 3-septate, septa often close together and end cells longer, seldom with 4 or more septa (up to 7), occasionally with vertical septa in central cells only or in every cell, order of septation variable, often 2:1:2, primary septum median and occasionally constricted; hyaline, smooth, without sheath or appendages.

Holotype: Great Britain: Easton, Norths., on dead twigs of rose (*Rosa* sp.), March 9, 1850 (K).

Exsiccatae: Austria: Fuckel, Fungi Rhenani 911 (Isotype of *Sphaeria corticola*, G, FH); Czechoslovakia: Welka, on *Prunus spinosa*, as *Metasphaeria corticola* f. *Pruni*, Oct. 3, 1912, Petrak, Fl. Boh et Mor. exsic. 61 (FH); Welka, on *Rosa canina*, as *Metasphaeria corticola* f. *Rosae*, Apr. 17, 1912, Petrak, Fl. Boh et Mor. exsic. 62 (FH); Ohrensdorf, on *Rubus thyrsoideus*, as *Metasphaeria corticola* f. *Rubi*, Sept. 25, 1911, Petrak, Fl. Boh et Mor. exsic. 63 (FH); Sweden: Lockerud, Wenenborg, on *Rubus fruticosus*, as *Leptosphaeria lejostega* (Ellis) Eliasson, Aug. 1892, Rehm, Asc. 1189 (FH); United States: New Jersey: Newfield, as *Sphaeria (Lept.) leiostega*, Ellis, N. American Fungi 888 (NY).

Other material examined: Austria: Nassau, on *Prunus domestica* and *P. spinosa*, Fuckel (Isotype, as *Metasphaeria corticola* (Fuckel) Sacc., FH); United States: Kansas: Rockport, Rooks Co., on *Cornus asperifolia*, as *Metasphaeria leiostega*, Dec. 24, 1894, E. Bartholomew (FH); Rooks Co., on *Ribes aureum*, as *Clypeosphaeria hendersonia* 2555, Mar. 15, 1899, E. Bartholomew (NY); Michigan: 573, Ann Arbor, on *Ribes frondium*, as *Metasphaeria leiostega*, Apr. 1, 1893, L.N. Johnson (NY); New Jersey: Newfield, on wild rose (*Rosa lucida* ?), May 6, 1879, J.B. Ellis (lectotype of *Sphaeria leiostega*, NY); Newfield, on *Viburnum lentago*, as *Sphaeria leiostega*, Dec. 1878, J.B. Ellis (NY); Newfield, Gloucester Co., on Hickory, as *Sphaeria leiostega* (NY); on *Staphylea trifolia*, as *Metasphaeria leiostega*, Dec. 23, 1891 (NY); on *Viburnum*, as *Metasphaeria leiostega* (NY); 1273, on wild currant, as *Metasphaeria leiostega*, Jan. 4, 1890 (NY); on *Comptonia*, as *Metasphaeria leiostega* Mar. 1890, J.B. Ellis (NY); Vineland, on *Vaccinium corymbosum*, as *Sphaeria leiostega*, Jan. 22, 1878; Jan. 10, 1880 (NY); New York: Washington Co., Vaughans, J. Vaughan's Copse, near Devines Woods, north of Hudson Falls, on *Ribes americanum (floridum)*, as *Metasphaeria leiostega*, Apr. 24, 1917, P.P. 25255, S.H. Burham (FH).

Comments: *Discostroma fuscella* is characterized by subepidermal perithecia with short protruding papillae, cylindrical asci with a J+ apical ring and hyaline, 3-septate, elliptical ascospores with broadly rounded ends. Certain collections have wider spores and vertical septa, most often in the central cells, but often also in the end cells. Most notably, vertical septa are found in the lectotype of *Sphaeria leiostega*. All other characters are identical to those of *D. fuscella*.

Discostroma corticola, the most common name of this fungus, is identical to the earlier named *Sphaeria fuscella*. Previous interpretations of *Sphaeria fuscella* have caused some confusion in the literature. The type material contains a fungus resembling *D. corticola*, with hyaline ascospores. However, it has been considered to be a 3-septate, brown-spored fungus because of Berkeley and Broome's (1852) description of ascospores as "pale brown, oblong-elliptic, obtuse, triseptate, sometimes slightly curved." In the accompanying Latin description they do not mention the color of the ascospores. On the type material (K), labeled "*Sphaeria fuscella* B & B. In *Rosa*, Easton, March 9, 1850," are three rose twigs, one of which is labeled (with a dotted line and a figure) as *Sphaeria (Subtectae) intermixta* B & B. The other two twigs contain abundant

material of the hyaline-spored fungus resembling *D. corticola*. Also on this material is a figure of *Sphaeria fuscella* showing an ascus and spores with "hyaline" written next to the spores. Wehmeyer (1957) suggested that a mixture of fungi in this and another collection of *S. fuscella* resulted in a confused description. He felt the name should be a nomen dubium and not used as a basis for later names. I believe, from the description and the fungus found on the type material, and from the figure on the type material, that Berkeley and Broome's confused description was not based on a mixture of fungi but was a miscommunication of the actual information. I believe they were aware that *S. fuscella* had hyaline, not brown spores; thus, it is suitable for use as a basis for later names.

Species incertae sedis

The following species were examined but could not be placed in any taxa with certainty because the type specimens contained no ascocarps and no other collections were available on which to base the descriptions.

•*Leptosphaeria eriobotryae* H. Sydow, P. Sydow & E. Butler, Annales Mycologici 9:409. 1911.

Holotype: Hab. in foliis *Eriobotrya japonicae*, Saharanpur, 27. 6. 1906, leg. Inayat (E.J. Butler no. 1365). (S) Isotype: (W, HCIO)

•*Leptosphaeria minima* (J.E. Duby) ex P.A. Saccardo, Michelia Commentarium Mycologicum Fungos in Primis Italicos Illustrans 2:320. 1881.

≡ *Sphaeria minima* J.E. Duby *in* C. Roumeguère, Fungi Selecti Gallici Exsiccati, Century 7, No. 694. Anno 1880. Nom. nud.

≡ *Mycotodea minima* (J.E. Duby ex P.A. Saccardo) W. Kirschstein *in* O.C. Schmidt, Kryptogamenflora der Mark Brandenburg und Angrenzender Gebiete herausgegeben von den Botanishen Verein der Provinz Brandenburg 7(3):432. 1938.

Isotype: Sur les feuilles du *Potentilla argentea* L., Mende, Prost. (G, FH, ILL, NY)

•*Leptosphaeria sorbi* A. Jaczewski, Annales Mycologici 1:30. 1903.

Holotype: in foliis vivis *Sorbi aucupariae*, IX. 18 1914 , Gjatsk. Smolensk. Gouv. Jaczewski. (LE)

Appendix: *Leptosphaeria* Species Described from the Rosaceae

The following is a list of all *Leptosphaeria* species described from the Rosaceae and the species' nomenclatural synomyms. This information is taken from Crane and Shearer (1991). The taxonomic synonyms applied herein and the herbaria contacted have been added. The fungal specimens cited in this dissertation were studied at or on loan from various herbaria. Requests were made to various herbaria for type material for all of the described species. Unfortunately, type material could not be located for all of the species because either the material was destroyed, lost, or not deposited at a certain institution, or the institutions involved did not reply or do not lend specimens. Abbreviations follow Holmgren et al. (1981).

L. abbreviata (M.C. Cooke) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:26. 1883. ≡*Sphaeria abbreviata* M.C. Cooke, Handbook of British Fungi, p. 893. 1871. On dead stems of *Rubus* sp., Rosaceae. Great Britain.
≡*Saccothecium sepincola* (E.M. Fries:E.M. Fries) E.M. Fries var. *abbreviata* S.M. Huhndorf, comb. nov.

L. aculeorum G. Passerini, Atti della R. Accademia dei Lincei Memoriae, Rome, Series 4, 6:458–459. (1889) 1890. On stems of *Rosa canina* L., Rosaceae. Italy. (non vidi). Type material was not found at PARMA, PISA, PAD.

L. arunci S.M. Zeller, Mycologia, Lancaster, Pennsylvania 19:134–135. 1927. On dead stems of *Aruncus silvestris* Kostel. (=*Aruncus dioicus* (Walter) Fernald), Rosaceae. United States (Oregon).
= *Kalmusia clivensis* (M.J. Berkeley & C.E. Broome) M.E. Barr.

L. cercocarpi H. Sydow & P. Sydow, Annales Mycologici, Berlin 5:339. 1907. On dead leaves of *Cercocarpus ledifolius* Nutt. ex Torr. & Gray, Rosaceae. United States.

L. concentrica J.B. Ellis & B.M. Everhart, The North American Pyrenomycetes. A Contribution to Mycologic Botany, p. 354. 1892. On leaves of *Malus* sp., Rosaceae. United States.
≡*Paraphaeosphaeria concentrica* (J.B. Ellis & B.M. Everhart) S.M. Huhndorf, comb. nov.

L. coniothyrium (L. Fuckel) P.A. Saccardo,Nuovo Giornale Botanico Italiano e Bolletino della Società Botanica Italiana, Firenze 7:317. 1875. ≡*Sphaeria coniothyrium* L. Fuckel, Symbolae Mycologicae, p. 115. 1870. ≡*Melanomma coniothyrium* (L. Fuckel) L. Holm, Symbolae Botanicae Upsalienses, Uppsala 14(3):56. 1957. On stems of *Alnus glutinosa* (L.) Gaertner, *Broussonetia* sp., *Chimonanthus* sp., *Kerria* sp., *Menispermum canadense* L., *Rosa* sp., *Rubus fruticosus* L., *Salix vitellina* L., *Sambucus nigra* L., Betulaceae, Moraceae, Calycanthaceae, Rosaceae, Menispermaceae, Salicaceae, Caprifoliaceae. Austria, France, Germany, Italy, Portugal.
≡*Kalmusia coniothyrium* (L. Fuckel) S.M. Huhndorf, comb. nov.

L. controversa (J. Desmazierès) V. Cesati & G. de Notaris, Commentario della Societa Crittogamologica Italiana, Milan 1:235. 1863. ≡*Sphaeria controversa* J. Desmazierès, Annales des Sciences Naturelles, Paris, Botanique, Series 2, 17:102. 1842. ≡*Diaporthe controversa* (J. Desmazierès) T.R.J. Nitschke *in* L. Fuckel, Symbolae Mycologicae Nachtrag 1:319. 1871. On plant stems, on dry branches of *Acer* sp., *Fraxinus* sp., *Rubus* sp., Aceraceae, Oleaceae, Rosaceae. France.
=*Diaporthe eres* T.R.J. Nitschke, fide L.E. Wehmeyer, The Genus *Diaporthe* Nitschke and its Segregates, p. 63. 1933.

L. corticola (L. Fuckel) P.A. Saccardo, Michelia Commentarium Mycologicum Fungos in Primis Italicos Illustrans 1:342. 1878; Fungi Italici autographice delineati (additis nonnullis extra-italicis asterisco notatis), Patavii, table 288. 1878. ≡*Sphaeria corticola* L. Fuckel, Symbolae Mycologicae, p. 114. 1870. ≡*Metasphaeria corticola* (L. Fuckel) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:166. 1883. ≡*Griphosphaeria corticola* (L. Fuckel) F. v. Hoehnel, Annales Mycologici, Berlin 16:87. 1918. ≡*Clathridium corticola* (L. Fuckel) R.A. Shoemaker & E. Mueller, Canadian Journal of Botany, Ottawa 42:404.

1964. ≡*Discostroma corticola* (L. Fuckel) I. Brockmann, Sydowia 28:313. 1975. On cortex of branchlets, on dry stems of *Cornus sanguinea* L., *Lonicera caprifolium* L., *Prunus baccata* Borkh., *Prunus domestica* L., *Prunus spinosa* L., *Rosa* sp., Caprifoliaceae, Rosaceae. Austria, Canada, Czechoslovakia, Germany, Hungary, Italy, Switzerland.
=*Discostroma fuscella* (M.J. Berkeley & C.E. Broome) S.M. Huhndorf, comb. nov.

L. dryadis E. Rostrup, Botanisk Tidsskrift, Kjøbenhavn 25:305. 1903. On decorticated wood stems and fruits of *Dryas octopetala* L., Rosaceae. Iceland.
=*Leptosphaeria dryadophila* S.M. Huhndorf, nom. nov.

L. dryadis E. Rostrup, Norske Ascomyceter i Christiania Universitetets Botaniske Museum. Christiania [Oslo] (I. Kommission Hos Jacob Dybwad), p. 24. 1904. [Issued in Skrifter Udgivne af Videnskabselskabet i Christiania. Mathematisk-naturvidenskabelig klasse. Christiania (Oslo) No. 274.] Non vidi. On upper surface of dried leaves of *Dryas octopetala* L., Rosaceae. Norway. (n. v.)

L. eriobotryae H. Sydow, P. Sydow & E. Butler, Annales Mycologici, Berlin 9:409. 1911. On leaves of *Eriobotrya japonica* (Thunb.) Lindley, Rosaceae. India.
Species incertae sedis.

L. fuscella (M.J. Berkeley & C.E. Broome) V. Cesati & G. de Notaris, Commentario della Società Crittogamologica Italiana, Milan 1:236. 1863. ≡*Sphaeria (Obtectae) fuscella* M.J. Berkeley & C.E. Broome, Annals and Magazine of Natural History, London, Series 2, 9:325. 1882. On dead twigs of *Rosa* sp., Rosaceae. Great Britain.
≡*Discostroma fuscella* (M.J. Berkeley & C.E. Broome) S.M. Huhndorf, comb. nov.

L. hazslinszkii P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:28. 1883. [Based on *Ditopella* sp., published by F.A. Hazslinszky, Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 20:217. 1870.] On dead branches of *Rosa* sp., Rosaceae. Rumania. (n. v.). Type material was not found at B, BP, F, FI, L, NBG, UPS, W, WAG. No reply from IBF, TNP. It is not known whether type material is at PAD because this institution has stopped lending specimens until further notice.

L. (*Clypeosphaeria*) *hendersoniae* (J.B. Ellis) M.C. Cooke, Grevillea, London 17:91. 1889. ≡*Sphaeria (Obtectae) hendersonia* J.B. Ellis *in* M.C. Cooke and J.B. Ellis, Grevillea, London 6:14–15. 1877. ≡*Clypeosphaeria hendersoniae* (J.B. Ellis) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:91. 1883. On canes of *Rubus* sp., Rosaceae. United States.
=*Kalmusia coniothyrium* (L. Fuckel) S.M. Huhndorf, comb. nov.

L. hollosiana L.E. Wehmeyer, Mycologia, Lancaster, Pennsylvania 55:319. 1963. ≡*Leptosphaeria maritima* L. Hollós, Annales Historico-Naturales Musei Nationalis Hungarici 5:46. 1907. Non *L. maritima* Ellis & Everhart, Non *L. maritima* Saccardo. On stems of *Biebersteinia emodii* Jaub. & Spach., *Potentilla argyrophylla* Wallich ex Lehm., *Potentilla fragarioides* L., *Triglochin maritima* L., *Trisetum spicatum* (L.) K. Richter, Geraniaceae, Gramineae, Juncaceae, Rosaceae. India. (n. v.). Type material was not found at BP, PAV, PRE.

L. leiostega (J.B. Ellis) J.B. Ellis, Catalogue of Plants Found in New Jersey. Geological Survey of New Jersey, Final Report of the State Geologist, Trenton 2(1):525. 1889. ≡*Sphaeria (Leptosphaeria) leiostega* J.B. Ellis, Bulletin of the Torrey Botanical Club (and Torreya), New York 8:91. 1881. On various dead twigs and limbs of *Carya* sp., *Rosa* sp., *Vaccinium* sp., Juglandaceae, Rosaceae, Ericaceae. United States (New Jersey).
=*Discostroma fuscella* (M.J. Berkeley & C.E. Broome) S.M. Huhndorf, comb. nov.

L. lejostega (J.B. Ellis) F. Hazslinszky, Matematikai és Természettudományi Közlemenyek Vonatkozólag a Hazai Viszonyokra, Budapest 25(2):148. 1892. ≡*Sphaeria (Leptosphaeria) leiostega* J.B. Ellis, Bulletin of the Torrey Botanical Club (and Torreya), New York 8:91. 1881. ≡*Metasphaeria lejostega* (J.B. Ellis) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:164. 1883. On branches of *Carya* sp., *Rosa* sp., *Vaccinium* sp., Juglandaceae, Rosaceae, Ericaceae. United States (New Jersey).

L. leucoplaca (K.F. Wallroth) E.A. Vainio, Acta Societatis pro Fauna et Flora Fennica, Helsingforsiae 49(2):143–144. 1921. ≡*Verrucaria leucoplaca* K.F. Wallroth, Flora Cryptogamica Germaniae 1:299. 1831. ≡*Pyrenula leucoplaca* (F.G. Wallroth) G.W. Koerber, Systema Lichenum Germaniae, p. 361. 1855. ≡*Verrucaria alba* H.A. Schrader var. *leucoplaca* (F.G. Wallroth) L.E. Schaerer *in* Enumeratio Critica Lichenum Europaeorum, Quos Ex Nova Methodo Digerit, p. 219. 1850. ≡*Eopyrenula leucoplaca* (K.F. Wallroth) R.C. Harris, The Michigan Botanist, Ann Arbor 12:19. 1973.

On bark of *Acer* sp., *Alnus* sp., *Carya* sp., *Corylus* sp., *Fraxinus* sp., *Juglans* sp., *Populus* sp., *Quercus* sp., *Salix* sp., *Sorbus* sp., *Tilia* sp., *Ulmus* sp., Aceraceae, Juglandaceae, Betulaceae, Oliaceae, Salicaceae, Fagaceae, Rosaceae, Tiliaceae, Ulmaceae. Finland. (n. v.). No reply from STR.

L. lucilla P.A. Saccardo, Nuovo Giornale Botanico Italiano e Bolletino della Società Botanica Italiana, Firenze 7:310–311. 1875. Indiscriminately on wilted leaves of *Pyrus communis* L., Rosaceae. Italy.
≡*Phaeosphaeria lucilla* (P.A. Saccardo) S.M. Huhndorf, comb. nov.

L. mandshurica M. Miura, Flora of Manchuria and East Mongolia, Part III, Cryptogams, Fungi (Contributions of the Southern Manchuria Railway Company 27):175. 1928. On leaves of *Pyrus malus* L. [as *Malus domestica* Borkh.], Rosaceae. China. (n. v.). Type material was not found at TI, TKB. No reply from TFM, TOFO, TNS.

L. minima (J.E. Duby) ex P.A. Saccardo, Michelia Commentarium Mycologicum Fungos in Primis Italicos Illustrans 2:320. 1881. ≡*Sphaeria minima* J.E. Duby *in* C. Roumeguère, Fungi Selecti Gallici Exsiccati, Century 7, No. 694. Anno 1880. Nom. nud. ≡*Mycotodea minima* (J.E. Duby ex P.A. Saccardo) W. Kirschstein *in* O.C. Schmidt, Kryptogamenflora der Mark Brandenburg und Angrenzender Gebiete herausgegeben von den Botanishen Verein der Provinz Brandenburg, Leipzig 7(3):432. 1938. On leaves of *Potentilla argentea* L., Rosaceae. France. Species incertae sedis.

L. miyakeana P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 24:999. 1928. ≡*Phaeosphaeria eriobotryae* I. Miyake, Botanical Magazine, Tokyo 27:41–42. 1913. ≡*Trematosphaerella eriobotryae* (I. Miyake) F.L. Tai, Sylloge Fungorum Sinicorum, p. 330. 1979. On leaves of *Eriobotrya japonica* (Thunb.) Lindley, Rosaceae. China. (n. v.). Type material was not found at TI, TKB. No reply from TFM, TOFO, TNS. It is not known whether type material is at PAD since this institution has stopped lending specimens until further notice.

L. mume K. Hara, Byôchu-gai Zasschi (Journal of Plant Protection), Tokyo 5:884. 1918. [As *mune* in original publication.] On dead branch of *Prunus mume* Sieb. & Zucc., Rosaceae. Japan. (n. v.). Type material was not found at TI, TKB. No reply from TFM, TOFO, TNS.

L. nashi (K. Hara) P.A. Saccardo *in* A. Trotter, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 24:999. 1928. ≡*Leptosphaerella nashi* K. Hara, Kajyu-byogai-ron Nihon-kankitsu-Kai, Schiznoka [Fruit Tree Diseases], pp. 142–145. 1916. ≡*Phaeospora nashi* (K. Hara) K. Hara, Jitsuyo-Sakumotsu-Byorigaku [Manual of Plant Pathology], p. 270. 1925. On leaves of *Pyrus sinensis* Hort., Rosaceae. Japan. (n. v.). Type material was not found at TI, TKB. No reply from TFM, TOFO, TNS.

L. (*Clypeosphaeria*) *notarisii* M.C. Cooke, Grevillea, London 17:91. 1889. ≡*Sphaeria clypeiformis* G. de Notaris, Memorie Della Accademia delle Scienze di Torino, Series 2, No. 7, p. 113. 1853; Micromycetes Italici Novi vel Minus Cogniti 7, p. 113. 1845. Non *Sphaeria clypeiformis* L.V. de Lacroix *in* G.L. Rabenhorst. ≡*Clypeosphaeria notarisii* L. Fuckel, Symbolae Mycologicae, p. 117. 1870. On barky runners of *Rubus fruticosus* L., Rosaceae. Italy.
=*Clypeosphaeria mamillana* (E.M. Fries: E.M. Fries) J.B.E. Lambotte.

L. obesula P.A. Saccardo *in* V. Mouton, Bulletin. Société R. de Botanique de Belgique, Bruxelles 26:176. 1887. On stems of *Acer pseudoplatanus* L., *Angelica* sp., *Spiraea ulmaria* L. (=*Filipendula ulmaria* Maxim.), Aceraceae, Umbelliferae, Rosaceae. Belgium. (n. v.). Type material was not found at DUKE. No reply from AUT, CGE, LD. It is not known whether type material is at PAD because this institution has stopped lending specimens until further notice.

L. oligotheca F. Petrak & H. Sydow, Annales Mycologici, Berlin 22:359. 1924. [Described from the type material of *Laestadia potentillae* E. Rostrup, Botanisk Tidsskrift, Kjøbenhavn 25:300. 1903.] On leaves of *Potentilla maculata* Pour. (=*Potentilla aurea* L.), Rosaceae. Denmark, Iceland.
=*Leptosphaerulina pulchra* (H.G. Winter) M.E. Barr.

L. (*Clypeosphaeria*) *osculanda* (C.G.T. Preuss) M.C. Cooke, Grevillea, London 17:91. 1889. ≡*Sphaeria osculanda* G.T. Preuss, Linnaea. Institut botanique de l'Université de Genève 26:713. 1853. ≡*Clypeosphaeria osculanda* (G.T. Preuss) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:91. 1883. On branches of *Rubus* sp., Rosaceae. Germany. (n. v.). Type material was not found at B.

L. oxyspora J. Feltgen, Vorstudien zu einer Pilz-Flora des Grossherzogthums, Luxemburg 1(2):165-166. 1901. On dry stems of *Rubus idaeus* L., Rosaceae. Luxemburg. (n. v.).

Type material is probably at LUX but was not obtained because the collections are undergoing reorganization.

L. pachytheca P.A. Saccardo, Nuovo Giornale Botanico Italiano e Bolletino della Società Botanica Italiana, Firenze, New Series 22:39. 1915. Nom. illeg. Art. 64.1. On dead branches of *Amygdalus communis* L. [=*Prunus dulcis* (Mill.) D.A. Webb], Rosaceae. Yugoslavia. (n. v.). It is not known whether type material is at PAD because this institution has stopped lending specimens until further notice.

L. (*Leptosphaerella*) *pomona* P.A. Saccardo, Nuovo Giornale Botanico Italiano e Bolletino della Società Botanica Italiana, Firenze 8:176. 1876. On upper surface of leaves of *Pyrus malus* L. (=*Malus domestica* Borkh.), Rosaceae. Italy.
≡*Phaeosphaeria pomona* (P.A. Saccardo) S.M. Huhndorf, comb. nov.

L. pomona P.A. Saccardo forma *transilvanica* A. Negru et I. Ditzu, Notulae Systematicae e Sectione Cryptogamica Instituti Botanici Nomine V.L. Komarov Academicae Scientiarum U.R.S.S., Petropolis 16:152–153. 1963. On fruits of *Crataegus monogyna* Jacq., Rosaceae. Rumania. (n. v.). Type material was not found at BUCM. No reply from BUC, BUCA, BUCF, CL.

L. poterii G. Passerini, Atti dell' Accademia Nazionale dei Lincei. Memoire, Rome, Series 4, 6:459. (1889) 1890. On wilted stems of *Poterium sanguisorba* L., Rosaceae. Italy. (n. v.). Type material was not found at PARMA, PISA, PAD.

L. praetermissa (P.A. Karsten) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:26. 1883. ≡*Sphaeria praetermissa* P.A. Karsten, Fungi Fenniae Exsiccati, Century 9, No. 852. Anno 1869. On dried canes of *Rubus idaeus* L., *Rubus odoratus* L., Rosaceae. Finland.

L. pruni N.N. Woronichin, Vestnik Tiflisskogo Botanicheskogo Sada, Tiflis (Moniteur du Jardin Botanique de Tiflis) 28:17–18. 1913. On living leaves of *Prunus domestica* L., Rosaceae. U.S.S.R. (Caucasus). (n. v.). Type material was not found at LE, LEP, TBI. No reply from TGM.

L. pulchra (H.G. Winter) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:53–54. 1883. ≡*Sphaerella pulchra* H.G. Winter, Hedwigia, Dresden 11:145–146. 1872. ≡*Mycodotea pulchra* (H.G. Winter) W. Kirschstein, Annales Mycologici, Berlin 34:201. 1936; Kryptogamenflora de Mark Brandenburg und Angrenzender Gebiete herausgegeben von den Botanischen Verein der Provinz Brandenburg, Leipzig 7(3):433. 1938. On dry stems and leaves of *Potentilla caulescens* L., Rosaceae. Austria. Type material was not found at B, CORD, IBF, JE, LZ, WRSL. No reply from FI, IB, TO, WAG.
≡*Leptosphaerulina pulchra* (H.G. Winter) M.E. Barr, Contributions de l'Institut Botanique de L'Université de Montréal 73:7. 1959.

L. puttemansii A. Maublanc, Bulletin de la Société Mycologique de France, Paris 21:88–89. 1905. On leaves of *Eriobotrya japonica* (Thunb.) Lindley, Rosaceae. Brazil. (n. v.). Type material was not found at IBI, PC, RSA-POM, SP. No reply from RBR.

L. rimicola (G.H. Otth) P.A. Saccardo, Hedwigia, Dresden 35:XXIX. 1896; Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 11:XXIX. 1896. ≡*Cladosphaeria rimicola* G.H. Otth, Mitteilungen der Naturforschenden Gesellschaft in Bern 1870:106. 1871. Nom inval. Art. 43.1. [The genus *Cladosphaeria* was validated in 1894.] On fallen branches of *Prunus avium* L., Rosaceae. Switzerland.
=*Melanomma pulvis-pyrius* (C.H. Persoon:E.M. Fries) L. Fuckel.

L. rostrupii P.A. Saccardo & D. Saccardo *in* P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 17:721. 1905. ≡*Leptosphaeria dryadis* E. Rostrup. Non Rostrup 1903. On upper surface of dried leaves of *Dryas octopetala* L., Rosaceae. Norway. (n. v.). It is not known whether type material is at PAD since this institution has stopped lending specimens until further notice.

L. rustica P.A. Karsten, Fungi Fenniae Exsiccati, Century 10, No. 964. Anno 1870.
≡*Metasphaeria rustica* (P.A. Karsten) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:157. 1883. On stems of *Spiraea ulmaria* L. (=*Filipendula ulmaria* Maxim.), Rosaceae. Finland.
=*Leptosphaeria doliolum* (C.H. Persoon:E.M. Fries) V. Cesati & G. de Notaris.

L. saccardiana J.H. Fabre, Annales des Sciences Naturelles, Paris, Botanique, Series 6, 9:89. 1878. ≡*Requienella saccardiana* (J.H. Fabre) J.H. Fabre, Annales des Sciences Naturelles, Paris, Botanique, Series 6, 15:56. 1883. On dried stems of *Crataegus oxyacantha* L., Rosaceae. France. (n. v.). Type material was not found at PC. No reply from L'HARMAS.

L. sanguisorbae P.A. Karsten *in* A.N. Berlese, Icones Fungorum Omnium Hucusque Cognitorum ad usum Sylloges Saccardianae

Adcommodatae 1:78. 1892. On branches of *Sanguisorba officinalis* L., Rosaceae. Germany. (n. v.). Type material was not found at H, UPS.

L. sanguisorbae P.A. Karsten, Enumeratio Fungorum et Myxomycetum in Lapponia Orientali Aestate 1861 Lectorum, p. 214. 1886; Notiser Sallskapets Pro Fauna et Flora Fordhandlingar 8:214. 1866. [As *Sphaeria (Leptosphaeria) sangvisorbae*.] On dead stems of *Sanguisorba polygama* F. Nyl., Rosaceae. U.S.S.R. (n. v.).

L. sepincola (E.M. Fries:E.M. Fries) H.G. Winter, Dr. L. Rabenhorst's Kryptogaman-Flora von Deutschland, Oesterreich und der Schweiz, Second edition, 1(2):473. 1885. ∫*Sphaeria sepincola* E.M. Fries, Observationes Mycologicae. Seu Descriptiones tam Novarum, quam Notabilium Fungorum Exhibitae a C.H. Persoon, Lipsiae 1:181. 1815; Systema Mycologicum Sistens Fungorum 2:498. 1823. [As *saepincola*.] ≡*Pringsheimia sepincola* (E.M. Fries:E.M. Fries) F. v. Hoehnel, Annales Mycologici, Berlin 18:97. 1920. ≡*Metasphaeria sepincola* (E.M. Fries:E.M. Fries) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:164. 1883. [As Fr? Fuckel.] ≡*Sphaerulina sepincola* (E.M. Fries:E.M. Fries) K.Starbäck, Botaniska Notiser, Lund 1890:117. 1890; Botanisches Zentralblatt, Jena & Dresden 46:261. 1891. ≡*Pleosphaerulina sepincola* (E.M. Fries:E.M. Fries) H. Rehm *in* F. v. Hoehnel, Annales Mycologici, Berlin 18:96. 1920. ≡*Sclerodothis sepincola* (E.M. Fries:E.M. Fries) F. Petrak, Annales Mycologici, Berlin 19:41. 1921. On dry stems of *Rosa* sp., *Rubus* sp., Rosaceae. Sweden.
≡*Saccothecium sepincola* (E.M. Fries:E.M. Fries) E.M. Fries, Summa Vegetabilium Scandinaviae, Seu Enumeratio, Systematica et Critica, Plantarum tum Cotyledonearum, Quam Nemearum Inter Mare Occidentale Et Album, Inter Eidoram et Nordkop, Hactenus Lectorum, una Cum Singulae Distributione Geographica, p. 398. 1849.

L. sieversiae (F.E. Clements) F. Petrak, Sydowia. Annales Mycologici, Horn, N.Ö. 6(1-4):6. 1952. ≡*Massaria sieversiae* F.E. Clements, Cryptogamae Formationum Coloradensium, Century III, No. 234. Anno 1906. Nom. nud. Art. 36.1. [Combination is not valid because the basionym is an invalidly published species.] On standing, dead stems of *Sieversia turbinata* (Rydb.) Greene, Rosaceae. U.S.A.
=*Diadema sieversiae* (C.H. Peck) S.M. Huhndorf, comb. nov.

L. sorbi A. Jaczewski, Annales Mycologici, Berlin 1:30. 1903. On leaves of *Sorbus aucuparia* L., Rosaceae. U.S.S.R.
Species incertae sedis.

L. spiraeae P.A. Karsten, Hedwigia, Dresden 27:260. 1888. On dry fallen branches of *Spiraea sorbifolia* L. (=*Sorbaria sorbifolia* A. Br.), Rosaceae. Finland. (n. v.). Type material was not found at H, UPS.

L. subcutanea (M.C. Cooke & J.B. Ellis) J.B. Ellis *in* N.L. Britton, Catalogue of Plants Found in New Jersey. Geological Survey of New Jersey, Final Report of the State Geologist, Trenton 2(1):525. 1889. ≡*Sphaeria (subtectae) subcutanea* M.C. Cooke & J.B. Ellis, Grevillea, London 7:41. 1878.
≡*Metasphaeria subcutanea* (M.C. Cooke & J.B. Ellis) P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:167. 1883. On decorticated limbs of *Pyrus communis* L., Rosaceae. United States. (New Jersey).
≡*Lophiostoma subcutanea* (M.C. Cooke & J.B. Ellis) S.M. Huhndorf, comb. nov.

L. superficialis F.A. Hazslinszky, Matematikai és Természettudományi Közlemenyek Vonatkozólag a Hazai Viszonyokra, Budapest 25(2):146. 1892. On unknown substrate of *Potentilla argentea* L., Rosaceae. Hungary. (n. v.). Type material was not found at B, BP, F, FI, L, NBG, UPS, W, WAG. No reply from IBF, TNP.

L. ternata F. Hazslinszky, Matematikai és Természettudományi Közlemenyek Vonatkozólag a Hazai Viszonyokra, Budapest 25(2):150. 1892. On branches of *Pyrus malus* L. (=*Malus domestica* Borkh.), Rosaceae. Hungary. (n. v.). Type material was not found at B, BP, F, FI, L, NBG, UPS, W, WAG. No reply from IBF, TNP.

L. thomasiana P.A. Saccardo & C. Roumeguère, Revue Mycologique, Toulouse 5:236. 1883. On dead runners of *Rubus* sp., Rosaceae. France. It is not known whether type material is at PAD because this institution has stopped lending specimens until further notice.
≡*Phaeosphaeria thomasiana* (P.A. Saccardo & C. Roumeguère) S.M. Huhndorf, comb. nov.

L. umbrosa G. Niessl *in* G.L. Rabenhorst, Fungi Europaei Exsiccati, Klotschii Herbarii vivi Mycologici Continuatio, Edition 3 (Edita Nova), Series 2, Century 20, No. 1934. Anno 1875; Just's Botanisch Jahresberichte, Berlin 3:262. 1887. ≡*Massaria umbrosa* (G. Niessl) H. Rehm *in* P.A. Saccardo, Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 9:761. 1891. On unknown substrate of *Actaea spicata* L., *Astrantia major* L.,

Gentiana asclepiadea L., *Solanum dulcamara* L., *Spiraea aruncus* L. (=*Aruncus dioicus* Fern.), Ranunculaceae, Umbelliferae, Gentianaceae, Solanaceae, Rosaceae. Austria.

L. vagabunda P.A. Saccardo, Nuovo Giornale Botanico Italiano e Bolletino della Società Botanica Italiana, Firenze 7:318. 1875. ≡*Sphaeria fuscella* P.A. Saccardo, Atti dell' Accademia Scientifica Veneto-Trentino-Istriana, Padova 2(1):145. 1873. [As *Sphaeria fuscella* M.J. Berkeley & C.E. Broome. Non *Leptosphaeria fuscella* (M.J. Berkeley & C.E. Broome) V. Cesati & G. de Notaris.] On branches of *Abies excelsa* (Lam.) Poiret, *Acer campestre* L., *Alnus glutinosa* (L.) Gaertner, *Ampelopsis heterophylla* (Thunb.) Sieb. & Zucc., *Clematis vitalba* L., *Cornus sanguinea* L., *Corylus avellana* L., *Dulcamara* sp., *Hypericum calycinum* L., *Kerria japonica* (L.) DC., *Quercus pedunculata* Ehrh., *Salix purpurea* L., Pinaceae, Aceraceae, Betulaceae, Vitaceae, Ranunculaceae, Cornaceae, Solanaceae, Guttiferae, Rosaceae, Fagaceae, Salicaceae. Italy. (n. v.). It is not known whether type material is at PAD because this institution has stopped lending specimens until further notice.

L. vagabunda P.A. Saccardo var. *divergens* P.A. Saccardo, Fungi Italici autographice delineati (additis nonnullis extra-italicis asterisco notatis), Patavii, No. 518. 1879; Sylloge Fungorum Omnium Hucusque Cognitorum Digessit P.A. Saccardo 2:31. 1883. On branches of *Kerria* sp., Rosaceae. Italy. (n. v.). It is not known whether type material is at PAD because this institution has stopped lending specimens until further notice.

L. vagabunda P.A. Saccardo var. *sarmenti* P.A. Saccardo, Fungi Italici autographice delineati (additis nonnullis extra-italicis asterisco notatis), Patavii, No. 428. 1879; Sylloge Fungorum Omnium Hucusque Congitorum Digessit P.A. Saccardo 2:31. 1883. On runners of *Rubus* sp., Rosaceae. Italy. (n. v.). It is not known whether type material is at PAD because this institution has stopped lending specimens until further notice.

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Index to Taxa

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Catalog of Types of the Illinois Natural History Survey Mycological Collections (ILLS)

J.L. Crane and Pamela P. Tazik

Illinois Natural History Survey Bulletin
Volume 34, Article 6
May 1992

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Illinois Natural History Survey, Lorin I. Nevling, Chief
A Division of the Illinois Department of Energy and Natural Resources

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Contents

Introduction

The mycological collections of the Illinois Natural History Survey and the University of Illinois at Urbana-Champaign originated with the rust collection of A.B. Seymour (1881–1886) and the powdery mildew collection of T.J. Burrill (1882–1885). These collections were integrated and housed in the Natural History Building on the campus of the University of Illinois at Urbana-Champaign until 1921, when the plant disease specimens were segregated and became the basis for the plant disease collection of the Illinois Natural History Survey. The program for collecting, identifying, and preserving plant disease specimens originated in 1881 and was expanded between 1921 and 1924 when special emphasis was placed on obtaining information on plant disease in the state. By 1924, 18,000 plant disease specimens had been added to the collection.

Gilbert L. Stout (1926–1930) was the first plant pathologist to concentrate on surveying plant disease in Illinois; he was succeeded by Gideon H. Boewe (1930–1966). Boewe's interest was the incidence, distribution, and severity of plant diseases. His specimens, together with those of Leo R. Tehon (1921–1954), who specialized in Ascomycetes and Fungi Imperfecti that cause plant disease, form a substantial part of the Survey's mycological collection.

James C. Carter (1934–1974) was an authority on the diseases of shade trees and ornamentals. His special interest was pathogenic fungi of woody ornamentals and he contributed numerous specimens to the mycological collection. In 1967, J. Leland Crane succeeded Boewe as mycologist, and to date he has contributed over 4,000 specimens of Ascomycetes and Fungi Imperfecti from decaying substrates in aquatic systems.

The Survey's mycological collection now contains approximately 300 type specimens, 800 Myxomycetes, 1,200 lower fungi, 10,000 Ascomycetes, 13,200 Fungi Imperfecti, 17,000 Basidiomycetes, and 5,000 lichens, for a total of 47,500 specimens.

This catalog provides information for each type specimen on the binomial, the full name and initials of the authorities, the place of publication, the category of type, substrate or host, locality data, date of collection, collector, and accession number. The categories of type specimens follow the Botanical Code (Grueter et al. 1988, Article 7). In this code, a nomenclatural **type** is that element to which the name of a taxon is permanently attached. A **holotype** is the one specimen or illustration used or designated by the author as the nomenclatural type. An **isotype** is any duplicate of the holotype. A **syntype** is any one of two or more specimens cited by the author when no holotype was designated, or when any one of two or more specimens was simultaneously designated as types. A **paratype** is a specimen or illustration cited in the protologue that is neither holotype or isotype, nor one of the syntypes if two or more specimens were simultaneously designated as types. A **lectotype** is a specimen or illustration selected from the original material to serve as a nomenclatural type when no holotype was indicated at the time of publication, or as long as it is missing. A **neotype** is a specimen or illustration selected to serve as nomenclatural type as long as all of the material on which the name of a taxon was based is missing.

Standardized, complete names of periodicals are cited following the system of Brown and Stratton (1963) and Porter and Koster (1970). The titles of books and pamphlets are cited according to Stafleu and Cowan (1976–1988). The scientific names of host plants are given as reported in the protologue of each type species. Plant genera were verified in Willis (1973) and Farr et al. (1979). Specific epithets of vascular plants were confirmed in Fernald (1950), Bailey and Bailey (1976), and Little (1979). The geographic location of species is restricted to information on the type specimen. Type specimens missing from the mycological collections are listed in the Appendix.

We express our sincere appreciation to Betty A. Nelson for technical assistance in the preparation of this manuscript.

Catalog of Types

Acrodictys martinii J.L. Crane & K.P. Dumont, Canadian Journal of Botany 53:846. 1975. **Isotype**: On rotted bark and wood along Rio Nueve Pasos, Dr. Luis Roure's property near Rosario, Puerto Rico, elevation 140 m, 17.VI.1970, leg. R.P. Korf et al., ILLS 35534. **Holotype**: NY.

Acrodontium myxomyceticola J.L. Crane & J.D. Schoknecht, Transactions of the British Mycological Society 79:346. 1982. **Isotype**: On *Stemonites fusca* A.W. Roth var. *fusca*, Territorio de Roraima, ca. 219 km north of Boa Vista, on the Boa Vista-Sta. Elena Venezuela Rd. (BR 174), Brazil, 1.XII.1977, leg. K.P. Dumont et al. BR-965, ILLS 42576. **Holotype**: NY.

Actinospora jamaicensis J.L. Crane & K.P. Dumont, Canadian Journal of Botany 53:843. 1975. **Isotype**: Ex CUP-MJ 128, on wet wood, along trail to Silver Hill Gap, near Woodcutter's Gap, vicinity of Newcastle, Portland Parish, Jamaica, 9.I.1971, leg. R.P. Korf et al., ILLS 35494. **Holotype**: NY.

Aniptodera chesapeakensis C.A. Shearer & M.A. Miller, Mycologia 69:894. 1977. **Holotype**: A dried culture, isolated from balsa wood submerged in the intake canal of the Potomac Electric Power Company, Electricity Generating Plant, Chalk Point, Maryland, 23.V.1973, leg. C.A. Shearer CS97-26, ILLS 36523. Culture from type: ATCC 32818.

Aristastoma concentrica L.R. Tehon, Mycologia 25:249. 1933. **Holotype**: On leaves of *Vigna sinensis* (L.) G. Engelmann, Metropolis, Massac County, Illinois, 12.X.1927, leg. G.L. Stout, ILLS 5453.

Ascochyta biguttulata E.Y. Daniels *in* L.R. Tehon and E.Y. Daniels, Mycologia 19:125. 1927. **Holotype**: On *Polygonum convolvulus* L., Urbana, Champaign County, Illinois, 11.X.1925, leg. E. Daniels, ILLS 2438.

Ascochyta elymi L.R. Tehon & E.Y. Daniels, Mycologia 19:124–125. 1927. **Holotype**: On *Elymus virginicus* L., Jacksonville, Morgan County, Illinois, 25.VII.1925, leg. L.R. Tehon, ILLS 3334.

Ascochyta maydis G.L. Stout, Mycologia 22:271–272. 1930. **Holotype**: On leaves of *Zea mays* L., Macomb, McDonough County, Illinois, 11.X.1926, leg. G.L. Stout, ILLS 19688. **Paratype**: Percy, Randolph County, Illinois, 9.XI.1927, leg. G.L. Stout, ILLS 21204.

Ascochyta negundinis L.R. Tehon, Mycologia 29:442–443. 1937. **Holotype**: On *Acer negundo* L., Mt. Carroll, Carroll County, Illinois, 22.VI.1935, leg. G.H. Boewe, ILLS 25193.

Ascochyta plantaginella L.R. Tehon, Mycologia 25:247. 1933. **Holotype**: On living leaves of *Plantago rugelii* J. Decaisne, Homer, Champaign County, Illinois, 6.VI.1929, leg. G.L. Stout, ILLS 22014.

Ascochyta rhodotypi H.W. Anderson, Transactions of the Illinois State Academy of Science 15:129. 1922. **Holotype**: On leaves of *Rhodotypos scandens* (C.P. Thunberg) T. Makino [as *R. kerrioides* P.F. von Siebold & J.G. Zuccarini in protologue], University of Illinois campus, Urbana, Champaign County, Illinois, 10.IX.1919 [as 15.IX.1919 in protologue], leg. H.W. Anderson, ILLS 4726.

Ascochyta zeae G.L. Stout, Mycologia 22:272. 1930. **Holotype**: On leaves of *Zea mays* L., Mt. Carmel, Wabash County, Illinois, 9.XI.1926, leg. G.L. Stout, ILLS 19581.

Asperisporium acori L.R. Tehon, Mycologia 40:321–322. 1948. **Holotype**: On *Acorus calamus* L., Urbana, Champaign County, Illinois, 17.VI.1926, leg. W.G. Solheim, ILLS 30124.

Brachysporiella dennisii J.L. Crane & K.P. Dumont, Canadian Journal of Botany 56:2613. 1978. **Isotype**: On unidentified stem, path between hotel and hotel's water source, Rancho Grande, Parq. Nac. Henry Pittier, Edo. Aragua, Venezuela, 3.VII.1971, leg. K.P. Dumont, J.H. Haines, & G.J. Samuels VE-1174, ILLS 36938, VEN. **Holotype**: NY.

Camposporium marylandicum C.A. Shearer, Mycologia 66:16. 1974. **Holotype**: On balsa wood [*Ochroma pyramidale* (A.J. Cavanilles) I. Urban] submerged in the Patuxent River at the Wildlife Refuge, Laurel, Maryland, 22.VII.1969 [as 22.V.1969 in protologue], leg. C.A. Shearer, ILLS 35538. **Paratype**: ILLS 35591.

Carpenterella molinea L.R. Tehon & H.A. Harris, Mycologia 33:128. 1941. **Holotype**: On *Ulmus americana* L., Madison, Wisconsin, 4.V.1932, leg. E.L. Champers, Wisconsin Department of Agriculture & Markets, ILLS 22722.

Catosphaeropsis caulivora L.R. Tehon, Mycologia 31:542. 1939. **Holotype**: On *Lespedeza stipulacea* C.J. Maximowicz, Crossville, White County, Illinois, 22.VII.1937, leg. G.H. Boewe, ILLS 26978. **Paratype**: Metropolis, Massac County, Illinois, 9.IX.1937, leg. G.H. Boewe, ILLS 26979.

Cercophora septentrionalis N. Lundqvist, Symbolae Botanicae Upsalienses 20(1):100. 1972. **Paratype**: Sweden, Gotland: Gerum par., 2 km E. of Hejdes in pine forest, on horse dung in moist chamber, Uppsala, 9.VI.1959, leg. N. Lundqvist 2126-e, ILLS 35156.

Cercospora abutilonis L.R. Tehon & E.Y. Daniels, Mycologia 17:246. 1925. **Holotype**: On *Abutilon theophrasti* F.C. Medicus, Spring Valley, Bureau County, Illinois, 17.VIII.1922, leg. C.L. Porter, ILLS 963.

Cercospora arborescentis L.R. Tehon & E.Y. Daniels, Mycologia 17:246. 1925. **Holotype**: On leaves of *Hydrangea arborescens* L., Thebes, Alexander County, Illinois, 17.VIII.1922, leg. P.A. Young, ILLS 599.

Cercospora cercidicola J.B. Ellis var. *coremioideas* L.R. Tehon, Mycologia 16:140. 1924. **Holotype**: On *Cercis canadensis* L., Boaz, Massac County, Illinois, 8.VIII.1922, leg. P.A. Young, ILLS 1129.

Cercospora difformis L.R. Tehon, Mycologia 40:322–323. 1948. **Holotype**: On *Viola* sp., wild, Vandalia, Fayette County, Illinois, 11.X.1944, leg. G.H. Boewe, ILLS 30224.

Cercospora hemerocallidis L.R. Tehon, Mycologia 16:139. 1924, [as *hemerocallis*]. **Holotype**: On *Hemerocallis fulva* L., Bloomfield, Johnson County, Illinois, 25.VII.1922, leg. P.A. Young, ILLS 2897.

Cercospora hyperici L.R. Tehon & E.Y. Daniels, Mycologia 19:127–128. 1927. **Holotype**: On *Hypericum adpressum* B.S. Barton, Bement, Piatt County, Illinois, 6.VII.1925, leg. L.R. Tehon, ILLS 13035.

Cercospora menthicola L.R. Tehon & E.Y. Daniels, Mycologia 17:247. 1925. **Holotype**: On leaves of *Mentha canadensis* L., Vandalia, Fayette County, Illinois, 14.VII.1924, leg. P.A. Young, ILLS 13699.

Cercospora nepetae L.R. Tehon, Mycologia 16:140. 1924. **Holotype**: On *Nepeta cataria* L., Ullin, Pulaski County, Illinois, 11.VIII.1922, leg. P.A. Young, ILLS 1419.

Cercospora paeoniae L.R. Tehon & E.Y. Daniels, Mycologia 17:247. 1925. **Holotype**: On leaves of *Paeonia officinalis* L., Prairie du Rocher, Randolph County, Illinois, 24.VIII.1922, leg. P.A. Young, ILLS 5645.

Cercospora plantaginella L.R. Tehon, Mycologia 16:139. 1924. **Holotype**: On *Plantago rugelii* J. Decaisne, Boaz, Massac County, Illinois, 8.VIII.1922, leg. P.A. Young, ILLS 1140.

Cercospora podophylli L.R. Tehon & E.Y. Daniels, Mycologia 19:128. 1927. **Holotype**: On *Podophyllum peltatum* L., Jersey County, Illinois, 2.VIII.1922, leg. C.O. Peake, ILLS 12950.

Cercospora psedericola L.R. Tehon, Mycologia 16:139. 1924. **Holotype**: On *Parthenocissus quinquefolia* (L.) J.E. Planchon, [as *Psedera*], Buckner, Franklin County, Illinois, 20.VII.1922, leg. P.A. Young, ILLS 2987.

Cercospora rhapontici L.R. Tehon & E.Y. Daniels, Mycologia 17:248. 1925. **Holotype**: On leaves of *Rheum rhaponticum* L., Coxeyville, Monroe County, Illinois, 24.VIII.1922, leg. P.A. Young, ILLS 5111.

Cercospora saccharini A.E. Liberta & G.H. Boewe, Mycologia 52:345–347. 1960. **Holotype**: On *Acer saccharinum* L., Metropolis, Massac County, Illinois, 15.X.1959, leg. G.H. Boewe, ILLS 33219.

Cercospora setariicola L.R. Tehon & E.Y. Daniels, Mycologia 19:128–129. 1927. **Holotype**: On *Setaria glauca* (L.) A. Beauvois, Macomb, McDonough County, Illinois, 16.VIII.1924, leg. P.A. Young, ILLS 11542. **Paratype**: Oquawka, Henderson County, Illinois, 15.IX.1924, leg. P.A. Young, ILLS 7905.

Cercospora silphii J.B. Ellis & B.M. Everhart var. *laciniati* L.R. Tehon & E.Y. Daniels, Mycologia 19:128. 1927. **Holotype**: On *Silphium laciniatum* L., Bement, Piatt County, Illinois, 6.VII.1925, leg. L.R. Tehon, ILLS 15262.

Cercospora sororiae L.R. Tehon, Mycologia 40:323–324. 1948. **Holotype**: On leaves of *Viola sororia* K.L. Willdenow, Kinderhook, Pike County, Illinois, 28.VI.1933, leg. G.H. Boewe, ILLS 30126.

Cercospora vignicaulis L.R. Tehon, Mycologia 29:436–437. 1937. **Holotype**: On *Vigna sinensis* (L.) G. Engelmann, Equality, Gallatin County, Illinois, leg. G.H. Boewe, 8.IX.1932, ILLS 23703 (with *Glomerella vignicaulis*).

Cercospora viminei L.R. Tehon, Mycologia 16:141. 1924. **Holotype**: On *Aster vimineus* J.B. Lamarck, Waltonville, Jefferson County, Illinois, 23.VI.1922, leg. P.A. Young, ILLS 2600.

Cercospora zeae-maydis L.R. Tehon & E.Y. Daniels, Mycologia 17:248. 1925. **Holotype**: On leaves of *Zea mays* L., McClure, Alexander County, Illinois, 29.VIII.1924, leg. P.A. Young, ILLS 4276.

Chaetomella tritici L.R. Tehon & E.Y. Daniels, Mycologia 17:242. 1925. **Holotype**: On inner surface of glumes of *Triticum aestivum* L., Waterloo, Monroe County, Illinois, 24.VIII.1922, leg. P.A. Young, ILLS 971.

Chaetopsina ludovicina J.L. Crane & J.D. Schoknecht, Canadian Journal of Botany 60:372. 1982. **Holotype**: On submerged, decayed? magnolia leaf, freshwater roadside swamp along Louisiana Route 51 about 20 miles north of New Orleans, St. John Baptist Parish, Louisiana, 1.VIII.1974, leg. J.L. Crane & J.D. Schoknecht, ILLS 40844.

Chaetoseptoria vignae L.R. Tehon, Mycologia 29:444. 1937. **Holotype**: On *Vigna sinensis* (L.) G. Engelmann, Eldorado, Saline County, Illinois, 10.IX.1934, leg. G.H. Boewe, ILLS 25080.

Chaetosphaeria aspergilloides M.E. Barr & J.L. Crane, Canadian Journal of Botany 57:835–836. 1979. **Isotype**: On decayed woody material, tropical greenhouse, Univ. Nac. Auton. de México, Distrito Federal, México, 7.IX.1972, leg. J.M. Trappe 3462, ILLS 37868. **Holotype**: NY.

Cladosporium calotropidis F.L. Stevens, Transactions of the Illinois State Academy of Science 10:207. 1917. **Isotype**: On *Calotropis procera* (W. Aiton) W.T. Aiton f., Guayanilla, Puerto Rico, VII.1915, leg. F.L. Stevens 9130, ILLS 41985. **Holotype**: BPI 70873.

Clavatospora stellatacula P. Kirk, Mycologia 61:178. 1969. **Isotype**: Isolated from submerged wood (*Pinus ponderosa* D. Douglas ex C. Lawson) in Chesapeake Bay, Fort Wood, Hampton, Virginia, leg. P. Kirk, VPI F-83, ILLS 34567. **Holotype**: P. Kirk 68-137, NY.

Clithris leucothoicola L.R. Tehon, Mycologia 31:676–677. 1939. **Holotype**: On *Leucothoe catesbei* (T. Walter) A. Gray [=*L. axillaris* (A.B. Lambert) D. Don], Stroudsburg, Pennsylvania, 24.V.1931, leg. B.H. Davis, ILLS 25091.

Codinaea gonytrichodes C.A. Shearer & J.L. Crane, Mycologia 63:245–247. 1971. **Holotype**: On fruit of *Carya* sp., cypress swamp, northwest of Karnak, Pulaski County, Illinois, 22.V.1969, leg. J.L. Crane 84-69, ILLS 34867. **Paratypes**: On balsa wood [*Ochroma pyramidale* (A.J. Cavanilles) I. Urban] submerged in Patuxent River at Naval Ordinance Laboratory Acoustics Facility, Brighton, Maryland, 22.IX.1967, C.A. Shearer & J.L. Crane, ILLS 34467; on samaras of *Acer* sp. and other decayed plant material, cypress swamp northwest of Karnak, Pulaski County, Illinois, 22.V.1969, leg. C.A. Shearer and J.L. Crane 94-69, ILLS 34868; saprophytic on seeds of *Liriodendron tulipifera* L., Forman Cypress Swamp, northwest of Belknap, Johnson County, Illinois, 18.XI.1969, C.A. Shearer & J.L. Crane 201-69, ILLS 34869.

Codinaea illinoensis A.D. Hewings & J.L. Crane, Mycotaxon. An International Journal Designed to Expedite Publication of Research on Taxonomy & Nomenclature of Fungi & Lichens 13:419–421. 1981. **Holotype**: On decayed wood, cypress swamp, northwest of Vienna, Johnson County, Illinois, 9.VII.1969, leg. J.L. Crane 98-69, ILLS 42169.

Codinaea matsushimae A.D. Hewings & J.L. Crane, Mycotaxon. An International Journal Designed to Expedite Publication of Research on Taxonomy & Nomenclature of Fungi & Lichens 13:423–425. 1981. **Holotype**: On exocarp of Juglandaceae (*Carya* sp.), Benson's Bluff, southeast of Goreville, Johnson County, Illinois, 4.IV.1969, leg. J.L. Crane 12-1-69, ILLS 42170. **Paratype**: On decayed wood, Elvira Cypress Swamp (Deer Pond), Johnson County, Illinois, 22 May 1969, leg. J.L. Crane, ILLS 42171.

Colletotrichum aeciicolum L.R. Tehon, Mycologia 25:254. 1933. **Holotype**: On unruptured peridia of aecidia of *Puccinia asterum* (L.D. von Schweinitz) F.D. Kern, in leaves of *Solidago canadensis* L., Beechville, Calhoun County, Illinois, 16.IX.1926, leg. G.L. Stout, ILLS 22416.

Colletotrichum dioscoreae L.R. Tehon, Mycologia 25:255. 1933. **Holotype**: On *Dioscorea villosa* L., Marlow, Jefferson County, Illinois, 7.IX.1926, leg. G.L. Stout, ILLS 22420.

Colletotrichum smilacinae L.R. Tehon & E.Y. Daniels, Mycologia 17:245–246. 1925. **Holotype**: On leaves of *Smilacina racemosa* (L.) R.L. Desfontaines, Goreville, Johnson County, Illinois, 22.VI.1924, leg. P.A. Young, ILLS 7259.

Colletotrichum smilacis L.R. Tehon, Mycologia 25:254–255. 1933. **Holotype**: On living leaves of *Smilax hispida* G. Muhlenberg, Olney, Richland County, Illinois, 21.IX.1932, leg. G.L. Stout, ILLS 22849.

Colletotrichum trillii L.R. Tehon, Mycologia 16:141. 1924. **Holotype**: On *Trillium recurvatum* Beck, Ryder, Jefferson County, Illinois, 23.VI.1922, leg. P.A. Young, ILLS 2350.

Confertopeltis asparagi L.R. Tehon, Mycologia 25:251. 1933. **Holotype**: On dry stems of *Asparagus officinalis* L., Villa Ridge, Pulaski County, Illinois, 10.XI.1927, leg. G.L. Stout, ILLS 7295.

Conioscypha varia C.A. Shearer, Mycologia 65:133. 1973. **Holotype**: A dried colony on cantino peptone yeast glucose agar, isolated from balsa wood [*Ochroma pyramidale* (A.J. Cavanilles) I. Urban] submerged in the Patuxent River at Triadelphia Reservoir, Brighton, Maryland, 18.XII.1968, leg. C.A. Shearer CS-125-6, ILLS 35119, culture from the type: ATCC 22765.

Coniothyrium fagi L.R. Tehon, Mycologia 25:247. 1933. **Holotype**: On leaves of *Fagus grandifolia* F. Ehrhart, Alto Pass, Union County, Illinois, 13.VI.1927, leg. G.L. Stout, ILLS 22555.

Coniothyrium negundinis L.R. Tehon & E.Y. Daniels, Mycologia 17:243. 1925. **Holotype**: On *Acer negundo* L., Urbana, Champaign County, Illinois, 3.VI.1922, leg. P.A. Young, ILLS 13413.

Coniothyrium radicicola L.R. Tehon, Mycologia 29:442. 1937. **Holotype**: On *Ulmus americana* L., Dayton, Ohio, XI.1934, leg. H.L. Jacobs, ILLS 24540.

Coniothyrium ulmi B.C. Tharp, Mycologia 9:116. 1917. **Isotypes**: On *Ulmus campestris* L., Bonham, Texas, 21.VIII.1916, ILLS 22805, TEX. **Holotype**: BPI.

Coniothyrium zeae G.L. Stout, Mycologia 22:273. 1930. **Holotype**: On *Zea mays* L., Putnam, Putnam County, Illinois, 6.X.1926, leg. G.L. Stout, ILLS 19686. **Paratype**: On leaves of *Zea mays* L., Casey, Clark County, Illinois, 24.X.1927, leg. G.L. Stout, ILLS 21159.

Cribopeltis citrullina L.R. Tehon, Mycologia 25:252. 1933. **Holotype**: On the fruit of *Citrullus vulgaris* H.A. Schrader, Spring Bay, Woodford County, Illinois, 30.IX.1927, leg. G.L. Stout, ILLS 22882.

Cryptostictis paeoniae L.R. Tehon & E.Y. Daniels, Mycologia 17:243–244. 1925. **Holotype**: On leaves of *Paeonia officinalis* L., Bloomfield, Johnson County, Illinois, 25.VII.1922, leg. P.A. Young, ILLS 6024.

Cylindrosporium quercinum J.C. Carter, Illinois Natural History Survey Bulletin 21(6):221. 1941. **Holotype**: On *Quercus imbricaria* A. Michaux, Carter, Marion County, Illinois, 17.IX.1936, leg. G.H. Boewe, ILLS 27081.

Cyphellopycnis pastinacea L.R. Tehon & G.L. Stout, Mycologia 21:189. 1929. **Holotype**: On *Pastinaca sativa* L., Arnold, Morgan County, Illinois, 20.VII.1926, leg. G.L. Stout, ILLS 13257.

Cytospora sambucina L.R. Tehon & G.L. Stout, Mycologia 19:122. 1927. **Holotype**: On *Sambucus canadensis* L., Oregon, Ogle County, Illinois, 26.VIII.1926, leg. C.L. Porter, ILLS 7426.

Cytospora sassafrasicola L.R. Tehon & E.Y. Daniels, Mycologia 19:122. 1927. **Holotype**: On *Sassafras variifolium* (R.A. Salisbury) O. Kuntze [=*S. albidum* (T. Nuttall) C.G. Nees von Esenbeck], Olney, Richland County, Illinois, 14.VI.1924, leg. P.A. Young, ILLS 12161.

Dactylaria fusiformis C.A. Shearer & J.L. Crane, Mycologia 63:243. 1971. **Holotype**: Isolated from balsa wood blocks [*Ochroma pyramidale* (A.J. Cavanilles) I. Urban] submerged in the Patuxent River at the Naval Ordnance Laboratory Acoustics Facility, Triadelphia Reservoir, Brighton, Maryland, 20.X.1967, leg. C.A. Shearer & J.L. Crane, ILLS 34519.

Dendrophoma zeae L.R. Tehon, Mycologia 25:246. 1933. **Holotype**: On arid leaves of *Zea mays* L., Clay City, Clay County, Illinois, 8.XI.1926, leg. G.L. Stout, ILLS 7742.

Diderma diadematum J.D. Schoknecht & J.L. Crane, Transactions of the British Mycological Society 70:146–147. 1978. **Holotype**: On submerged, decayed leaves of angiosperms (*Acer* sp.) and *Taxodium distichum* (L.) L.C. Richard, Elvira Cypress Swamp (Deer Pond), Johnson County, Illinois, 9.III.1977, leg. J.D. Schoknecht & J.L.Crane, ILLS 36664. **Isotype**: NY, TER, K. **Paratypes**: ILLS 36883, ILLS 36884, ILLS 36885.

Diplodia acericola L.R. Tehon & G.L. Stout, Mycologia 21:190. 1929. **Holotype**: On *Acer saccharum* H. Marshall, Mt. Pleasant, Union County, Illinois, 7.VII.1926, leg. G.L. Stout, ILLS 14104.

Diplodia sambuci L.R. Tehon & E.Y. Daniels, Mycologia 19:125. 1927. **Holotype**: On *Sambucus canadensis* L., Oregon, Ogle County, Illinois, 26.VIII.1922, leg. C.L. Porter, ILLS 7073.

Diplodia ulmi J.B. Dearness, Mycologia 8:102. 1916. **Isotype**: On dead branchlets of *Ulmus americana* L., London, Ontario, X.1903, J.B. Dearness 3052, ILLS 22806.

Diplopeltis sassafrasicola L.R. Tehon & G.L. Stout, Mycologia 21:193. 1929. **Holotype**: On *Sassafras albidum* (T. Nuttall) C.G. Nees von Esenbeck, Thebes, Alexander County, Illinois, 17.VII.1922, leg. P.A. Young, ILLS 581.

Discosia potentillae L.R. Tehon, Mycologia 25:253. 1933. **Holotype**: On leaves of *Potentilla canadensis* L., Marlow, Jefferson County, Illinois, 7.IX.1926, leg. L.R. Tehon, ILLS 22390.

Dothistroma pini R.L. Hulbary, Illinois Natural History Survey Bulletin 21(7):236. 1941. **Holotype**: On *Pinus nigra* J. Arnold var. *austrica* (F. Hoess) H. Badoux, Waterman, DeKalb County, Illinois, 29.XI.1938, leg. J.C. Carter, ILLS 27093.

hragmia boewei J.L. Crane, Mycologia 64:658–661. 1972. **Holotype**: On decayed plant material, Grantsville Cypress Swamp, east of Grantsville, Johnson County, Illinois, 2.V.1969, leg. J.L. Crane 64-69, ILLS 34948.

Endophragmia triseptata C.A. Shearer, J.L. Crane & M.A. Miller, Mycologia 68:184–186. 1976. **Holotype**: On decaying submerged wood, Elvira Cypress Swamp (Deer Pond), Johnson County, Illinois, 27.VI.1970, leg. J.L. Crane 28-70, ILLS 36154. **Isotype**: NY.

Epicoccum nigrum J.H. Link, Observationes in Ordines Plantarum Naturales, Dissertatio Secunda 2:32. 1815. **Isotype**: Communicated by H. Sydow, date unknown, ILLS 24668.

Epidermella hansbroughii L.R. Tehon, Mycologia 31:688–689. 1939. **Holotype**: On *Rubus idaeus* L. var. *aculeatissimum* E.A. von Regel & H.S. Tiling, Bennington, Vermont, 8.VII.1937, leg. J.R. Hansbrough 3069, ILLS 25862.

Erikssonia protii E.K. Cash, Mycologia 35:634–635. 1943. **Holotype**: On *Protium asperum* P.C. Standley, Almirante, Panama, 28.VIII.1940, leg. R.C. Lorenz 3070, BPI 71385. **Isotype**: ILLS 41994.

Exilispora plurisepta L.R. Tehon & E.Y. Daniels, Mycologia 19:113. 1927. **Holotype**: On *Erigeron* sp., McNabb, Putnam County, Illinois, 28.VI.1922, leg. C.L. Porter, ILLS 8404.

Exophoma astericola L.R. Tehon, Mycologia 21:188–189. 1929. **Holotype**: On *Aster tardiflorus* L., Paris, Edgar County, Illinois, 4.XI.1926, leg. G.L. Stout, ILLS 19386.

Fusicoccum elaeagni J.C. Carter & C.M. Sacamano, Mycologia 59:537. 1967. **Holotype**: On *Elaeagnus angustifolia* L., J.F. Neil property, 9007 McKnight Woods, Clayton, Missouri, 18.VI.1963, leg. C.M. Sacamano, ILLS 34453.

Gloeosporium impatientis H.W. Anderson, Transactions of the Illinois State Academy of Science 15:128. 1922. **Holotype**: On *Impatiens biflora* T. Walter, Brownfield Woods, Urbana, Champaign County, Illinois, 19.VIII.1921, leg. H.W. Anderson, ILLS 4722.

Glomerella vignicaulis L.R. Tehon, Mycologia 29:435–436. 1937. **Holotype**: On *Vigna sinensis* (L.) S.L. Endlicher, Equality, Gallatin County, Illinois, 8.IX.1932, leg. G.H. Boewe, ILLS 23703. **Paratypes**: Carmi, White County, Illinois, 10.IX.1934, leg. G.H. Boewe, ILLS 24809; Olmstead, Pulaski County, Illinois, 17.IX.1933, leg. G.H. Boewe, ILLS 25450.

Grovesinia pyramidalis M.N. Cline, J.L. Crane & S.D. Cline, Mycologia 75:991. 1983. **Holotype**: Dried sclerotia and apothecia from sterilized vermiculite in deep dishes and derived dried cultures of micro- and macroconidia, Champaign County, Illinois, VIII.1982, leg. M.N. Cline, ILLS 43169. **Isotypes**: BPI, CUP, IMI.

Gymnosporangium vauqueliniae W.H. Long & L.N. Goodding, Mycologia 31:671–673. 1939. **Paratype**: On *Juniperus monosperma* (G. Engelmann) C.S. Sargent, Superstition Mountain, Arizona, 5.V.1939, leg. L.N. Goodding 8371, ILLS 41921.

Halosarpheia cincinnatula C.A. Shearer & J.L. Crane, Botanica Marina 23:613. 1980. **Holotype**: On balsa wood [*Ochroma pyramidale* (A.J. Cavanilles) I. Urban] submerged in intake canal (Patuxent River) of the Potomac Electricity Generating Plant at Chalk Point, Ann Arundel County, Maryland, 16.VI.1969, leg. C.A. Shearer C.S. 93-2, ILLS 39006.

Halosarpheia retorquens C.A. Shearer & J.L. Crane, Botanica Marina 23:608–610. 1980. **Holotype**: On dried culture of alfalfa (*Medicago sativa* L.), originally isolated from balsa wood [*Ochroma pyramidale* (A.J. Cavanilles) I. Urban] submerged in the Sangamon River below the sewage treatment plant at Decatur, Macon County, Illinois, 21.X.1975, leg. J.L. Crane & C.A. Shearer C.S. 549-2, ILLS 38994.

Helminthosporium zeicola G.L. Stout, Mycologia 22:273–274. 1930. **Holotype**: On stalks of *Zea mays* L., Dixon, Lee County, Illinois, 27.IX.1926, leg. G.L. Stout, ILLS 19884. **Paratypes**: Eichorn, Hardin County, Illinois, 21.X.1926, leg. G.L. Stout, ILLS 20180; Shelbyville, Shelby County, Illinois, 16.XI.1926, leg. G.L. Stout, ILLS 20181; Mount Carroll, Carroll County, Illinois, 27.IX.1926, leg. G.L. Stout, ILLS 20182.

Hyalocylindrophora venezuelensis J.L. Crane & K.P. Dumont, Canadian Journal of Botany 56:2616. 1978. **Isotype**: On unidentified wood, 30 km north of San Cristobal, on San Cristobal-LaGrita Road, Edo. Tachira, Venezuela, 28.VII.1971, leg. K.P. Dumont, G.J. Samuels, and L. Borjas VE-3249, ILLS 36940. **Holotype**: NY.

Hydnellum pineticola K.A. Harrison, Canadian Journal of Botany 42:1226. 1964. **Isotype**: North of Sheephead Lake, Chippewa County, Michigan, 23.VIII.1961, leg. A.H. Smith & K.A. Harrison, A.H.S. 63973, ILLS 47446.

Hydnum calvatum K.A. Harrison var. *calvatum*, Canadian Journal of Botany 42:1216–1217. 1964. **Paratype**: Under spruce, Middle Fork of Lake Fork Creek, Idaho National Forest, Valley County, Idaho, 5.VIII.1941, leg. A.H. Smith 16023, ILLS 44310. **Holotype**: MICH.

Hypoderma apocyni L.R. Tehon, Mycologia 31:679–680. 1939. **Holotype**: On dead stems of *Apocynum medium* E.L. Greene, Pine Plains, New York, 27.VIII.1935, leg. J.R. Hansbrough 1766, ILLS 25094.

Hypoderma caryae L.R. Tehon, Mycologia 31:680–681. 1939. **Holotype**: On fallen petioles of *Carya glabra* (P. Miller) R. Sweet, Hamilton, Massachusetts, 7.XI.1935, leg. H.G. Eno, communicated by J.R. Hansbrough 1772, ILLS 25095.

Hysterium pulcherrimum L.R. Tehon & P.A. Young, Mycologia 16:31–32. 1924. **Holotype**: On bark of *Platanus occidentalis* L., White Heath, Piatt County, Illinois, 12.V.1923, leg. P.A. Young, ILLS 4949.

Intercalarispora nigra J.L. Crane & J.D. Schoknecht, Canadian Journal of Botany 61:2243–2244. 1983. **Holotype**: On decayed wood submerged in Forman Cypress Swamp, NW of Belknap, Johnson County, Illinois, 29.X.1970, leg. J.L. Crane 203-69, ILLS 43047. **Isotype**: NY. **Paratypes**: ILLS 43045, ILLS 43046, ILLS 43048.

Kaskaskia gleditsiae G.L. Born & J.L. Crane, Phytopathology 62:927–929. 1972. **Holotype**: Parasitic on *Gleditsia triacanthos* L. var. *inermis* C.K. Schneider, Freer Gymnasium, University of Illinois, Urbana, Champaign County, Illinois, leg. J.C. Carter, 17.VI.1968, ILLS 34832. **Isotype**: IMI 151725, NY, culture from the type: ATCC 22647.

Labrella aspidistrae L.R. Tehon & E.Y. Daniels, Mycologia 19:126. 1927. **Holotype**: On *Aspidistra* sp., Libertyville, Lake County, Illinois, 9.VI.1922, leg. C.L. Porter, ILLS 7648.

Lactarius areolatus L.R. Hesler & A.H. Smith, North American Species of *Lactarius*, University of Michigan Press, Ann Arbor, pp. 515–516. **Paratypes**: Highland Recreation Area, Oakland County, Michigan, 10.VIII.1972, leg. A.H. Smith & N.S. Weber, A.H.S. 81439, ILLS 47447; 27.VIII.1972, leg. A.H. Smith & N.S. Weber, A.H.S. 81784, ILLS 47452; Mill Lake, Waterloo Recreation Area, Washtenaw County, Michigan, 11.VIII.1972, leg. A.H. Smith & N.S. Weber, A.H.S. 81456, ILLS 47451; Gorman Lake, Washtenaw County, Michigan, 20.VIII.1972, leg. A.H. Smith & N.S. Weber, A.H.S. 81635, ILLS 47448; Cedar Lake, Waterloo Recreation Area, Washtenaw County, Michigan, 11.VII.1973, leg. A.H. Smith & N.S. Weber, A.H.S. 84178, ILLS 47450; Haven Hill, Highland Recreation Area, Oakland County, Michigan, 12.VIII.1973, leg. A.H. Smith & N.S. Weber, A.H.S. 84424, ILLS 47449.

Lepidopterella palustris C.A. Shearer & J.L. Crane, Transactions of the British Mycological Society 75:194–195. 1980. **Holotype**: On unidentified submerged twigs and cultured on alfalfa (*Medicago* sp.) stems, Elvira Cypress Swamp, Johnson County, Illinois, 3.VIII.1977, leg. J.L. Crane & C.A. Shearer CS-470, ILLS 38990. Culture from type: ATCC 38017. **Isotype**: NY. **Paratype**: On twigs submerged in Elvira Cypress Swamp, Johnson County, Illinois, 6 VIII 1974, leg. C.A. Shearer & J.L. Crane CS-470-1, ILLS 38991.

Leptosphaeria maydis G.L. Stout, Mycologia 22:275. 1930. **Holotype**: On leaves of *Zea mays* L., Vandalia, Fayette County, Illinois, 6.XI.1926, leg. G.L. Stout, ILLS 19423. **Paratypes**: Shelbyville, Shelby County, Illinois, 6.XI.1926, leg. G.L. Stout, ILLS 19669; Moline, Rock Island County, Illinois, 8.X.1926, leg. G.L. Stout, ILLS 19716; Streator, La Salle County, Illinois, 23.IX.1926, leg. G.L. Stout, ILLS 19671; Elgin, Kane County, Illinois, 24.IX.1926, leg. G.L. Stout, ILLS 19725; Mt. Carmel, Wabash County, Illinois, 6.X.1927, leg. G.L. Stout, ILLS 21223.

Leptosphaeria variiseptata G.L. Stout, Mycologia 22:276–277. 1930. **Holotype**: On leaves of *Zea mays* L., Roscoe, Winnebago County, Illinois, 25.IX.1926, leg. G.L. Stout, ILLS 19726. **Paratype**: Carmi, White County, Illinois, 10.XI.1926, leg. G.L. Stout, ILLS 19727.

Leptosphaeria zeae G.L. Stout, Mycologia 22:277. 1930. **Holotype**: On leaves of *Zea mays* L., Sandoval, Marion County, Illinois, 6.XI.1926, leg. G.L. Stout, ILLS 19421. **Paratype**: Clay City, Clay County, Illinois, 8.XI.1926, leg. G.L. Stout, ILLS 19422.

Leptosphaerulina vignae L.R. Tehon & G.L. Stout, Phytopathology 18:703. 1928. **Holotype**: On *Vigna sinensis* Hassk., Huey, Clinton County, Illinois, 5.IX.1927, leg. G.L. Stout, ILLS 20937.

Leptostroma querci L.R. Tehon, Mycologia 29:446. 1937. **Holotype**: On leaves of *Quercus imbricaria* A. Michaux, Ramsey, Fayette County, Illinois, 7.VI.1927, leg. L.R. Tehon, ILLS 9455.

Leptostromella solani L.R. Tehon, Mycologia 40:317–318. 1948. **Holotype**: On stems of *Solanum carolinense* L., LeRoy, McLean County, Illinois, 11.X.1943, leg. G.H. Boewe, ILLS 30051.

Leptothyriella liquidambaris L.R. Tehon & G.L. Stout, Mycologia 21:192–193. 1929. **Holotype**: On *Liquidambar styraciflua* L., Olmstead, Pulaski County, Illinois, 9.VIII.1922, leg. P.A. Young, ILLS 1445.

Leptothyrium anthelmintici L.R. Tehon, Mycologia 40:314–315. 1948. **Holotype**: On dead stems of *Chenopodium ambrosioides* L. var. *anthelminticum* (L.) A. Gray, Harrisburg, Saline County, Illinois, 16.VIII.1943, leg. G.H. Boewe, ILLS 30049.

Leptothyrium avenae L.R. Tehon, Mycologia 40:315. 1948. **Holotype**: On *Avena sativa* L., Woodford, Woodford County, Illinois, 1.VII.1938, leg. G.H. Boewe, ILLS 29926.

Leptothyrium brunnichiae L.R. Tehon, Mycologia 16:136. 1924. **Holotype**: On *Brunnichia cirrhosa* J. Gaertner, Karnak, Pulaski County, Illinois, 8.VIII.1922, leg. P.A. Young, ILLS 1120.

Leptothyrium fimbriatum L.R. Tehon, Mycologia 40:315–317. 1948. **Holotype**: On leaves of *Smilax hispida* (G. Muhlenberg) M.L. Fernald, Topeka, Mason County, Illinois, 20.X.1937, leg. G.H. Boewe, ILLS 30050.

Leptothyrium maximum L.R. Tehon & E.Y. Daniels, Mycologia 17:245. 1925. **Holotype**: On diseased twigs of *Acer negundo* L., Urbana, Champaign County, Illinois, 3.VI.1922, leg. P.A. Young, ILLS 1795.

Leptothyrium zeae G.L. Stout, Mycologia 22:278. 1930. **Holotype**: On leaves of *Zea mays* L., Vandalia, Fayette County, Illinois, 6.XI.1926, leg. G.L. Stout, ILLS 19445. **Paratypes**: Sullivan, Moultrie County, Illinois, 16.XI.1926, leg. G.L. Stout, ILLS 19670; Belleview, Calhoun County, Illinois, 7.XI.1927, leg. G.L. Stout, ILLS 21154.

Lophodermina melaleucaum (E.M. Fries:E.M. Fries) F. v. Höhnel var. *epiphyllum* S.M. Zeller, Mycologia 26:293. 1934. **Holotype**: On *Vaccinium ovatum* F.T. Pursh, Waldport, Oregon, X.1929, leg. S.M. Zeller, ILLS 24405.

Lophodermina septata L.R. Tehon, Illinois Biological Monographs, University of Illinois at Urbana-Champaign 13(4):109. 1935. **Holotype**: On *Picea sitchensis* (A.H.G. Bongard) E.A. Carrière, Knappa, Clatsop County, Oregon, 3.V.1919, leg. E.J. Perkins, communicated by W.W. Wagener, ILLS 23480.

Lophodermium antarcticum C.L. Spegazzini, Fungi Fuegani No. 304. 1887; Boletin de la Academia Nacional de Ciencias en Cordoba 11:249–250. 1887. **Isotype**: On *Rostkovia grandiflora* W.J. Hooker, Staten Island, Tierra del Fuego, Argentina, Mart. 1882, leg. C.L. Spegazzini, ILLS 23567 as a microscopic preparation. **Holotype**: LPS.

Lophodermium camelliae S.C. Teng, Sinensia. Special Bulletin of the Metropolitan Museum of Natural History 4:138. 1933. **Isotype**: On fallen leaves of *Camellia* sp., Teng's garden, Foochow, Fukien Province, China, 18.VIII.1933, leg. S.C. Teng 1904, ILLS 25087.

Lophodermium claviligerum C.L. Spegazzini, Fungi Fuegani No. 305. 1887; Boletin de la Academia Nacional de Ciencias en Cordoba 11:250. 1887. **Presumed isotype**: On *Pernettia mucronata* (L. f) C. Gaudichaud-Beaupré ex K. Sprengel, Staten Island, Tierra del Fuego, Argentina, date unknown [as Mart. 1882 in protologue], leg. unknown, ILLS 23564.

Lophodermium danthoniae L.R. Tehon, Mycologia 31:690–691. 1939. **Isotype**: On dead leaves of *Danthonia spicata* (L.) A. Beauvois, Brule, Wisconsin, 11.VIII.1934, leg. J.J. Davis, ILLS 25090. **Holotype**: WIS. **Paratype**: Carbondale, Jackson County, Illinois, 28.IV.1938, leg. G.H. Boewe, ILLS 27027.

Lophodermium fuegianum C.L. Spegazzini, Fungi Fuegiani No. 306. 1887; Boletin de la Academia Nacional de Ciencias en Cordoba 11:250. 1887. **Presumed isotype**: On *Rostkovia grandiflora* W.J. Hooker, Staten Island, Tierra del Fuego, Argentina, date unknown [as Agaia, Jun. 1882 in protologue], leg. unknown, ILLS 23565 as a microscopic preparation.

Lophodermium leptothecium C.L. Spegazzini, Fungi Guaranitici I, No. 307. 1885; Anales de la Sociedad Cientifica Argentina 19:261. 1885. **Isotype**: On *Laurinea* sp., Guarapi, Paraguay, VI.1883, leg. B. Balansa, ILLS 23569. **Holotype**: LPS.

Lophodermium rosae S.C. Teng, Sinensia. Special Bulletin of the Metropolitan Museum of Natural History, 4:138–139. 1933. **Isotype**: On *Rosa* sp. (on dead twigs), Heng-shan, Hunan Province, China, IX.1933, leg. C.I. Shen 390, communicated by S.C. Teng, ILLS 25086. **Holotype**: Metropolitan Museum Academia Sinica, Nanjing, China.

Lophodermium sesleriae A. Hilitzer, Vědecké spisy Vydávané Československou Akademii Zemědělskou 3:91. 1929. **Isotype**: On *Sesleria caerulea* (L.) P. Arduino, Prague, Czechoslovakia, 13.X.1927, leg. A. Hilitzer, ILLS 24394.

Lophodermium subtropicale C.L. Spegazzini, Anales del Museo Nacional de Historia Natural de Buenos Aires 23:88–89. 1912; Mycetes Argentinenses, Series 6, No. 1443. 1912. **Isotype**: On *Psidium* sp., Puerto León, Missiones, Argentina, IX.1909, leg. unknown, ILLS 23566 as a microscopic preparation. **Holotype**: LPS.

Lophodiscella asparagi L.R. Tehon, Mycologia 25:253. 1933. **Holotype**: On arid stems of *Asparagus officinalis* L., Villa Ridge, Pulaski County, Illinois, 10.XI.1927, leg. G.L. Stout, ILLS 7576. **Paratypes**: Anna, Union County, Illinois, 10.XI.1927, leg. G.L. Stout, ILLS 7597; Alto Pass, Union County, Illinois, 10.XI.1927, leg. G.L. Stout, ILLS 7603; 26.XI.1927, leg. G.L. Stout, ILLS 7740.

Luttrellia estuarina C.A. Shearer, Mycologia 70:692–693. 1978. **Holotype**: On balsa wood [*Ochroma pyramidale* (A.J. Cavanilles) I. Urban] from intake canal of Potomac Electric Power Company, Electricity Generating Plant, Chalk Point, Patuxent River, Maryland, 26.VII.1973, leg. C.A. Shearer CS-80-4, ILLS 36979.

Macrophoma cercis L.R. Tehon & G.L. Stout, Mycologia 21:188. 1929. **Holotype**: On *Cercis canadensis* L., Venedy, Washington County, Illinois, 8.IX.1926, leg. G.L. Stout, ILLS 19972.

Macrophoma oblongata L.R. Tehon, Mycologia 29:438. 1937. **Holotype**: On *Poa pratensis* L., Rushville, Schuyler County, Illinois, 2.VIII.1935, leg. G.H. Boewe, ILLS 25381.

Macrophoma phlei L.R. Tehon & G.L. Stout, Mycologia 21:188. 1929. **Holotype**: On *Phleum pratense* L., Wayne City, Wayne County, Illinois, 8.XI.1926, leg. G.L. Stout, ILLS 19413.

Macrophoma rubi L.R. Tehon, Mycologia 29:441. 1937. **Holotype**: On *Rubus idaeus* L. var. *strigosus* (A. Michaux) L.J. Maximowicz (Latham raspberry, cultivated), Barry, Pike County, Illinois, 30.VIII.1934, leg. G.H. Boewe, ILLS 24802.

Macrophoma secalina L.R. Tehon, Mycologia 29:438–440. 1937. **Holotype**: On dead leaves and sheaths of *Secale cereale* L., Liberty, Adams County, Illinois, 23.VI.1931, leg. G.H. Boewe, ILLS 23913. **Paratype**: Westville, Vermilion County, Illinois, 3.VII.1935, leg. G.H. Boewe, ILLS 25073.

Marssonina salicina L.R. Tehon, Mycologia 25:255–256. 1933. **Holotype**: On leaves of *Salix nigra* H. Marshall, Lincoln, Logan County, Illinois, 18.VI.1930, leg. L.R. Tehon, ILLS 22258.

Masoniomyces claviformis J.L. Crane & K.P. Dumont, Canadian Journal of Botany 53:847. 1975. **Isotype**: On wood, Dolphin Head, Hanover Parish, Jamaica, 22.I.1971, leg. R.P. Korf et al., 715, ILLS 35742. **Holotype**: NY.

Melanospora interna L.R. Tehon & G.L. Stout, Mycologia 21:181–182. 1929. **Holotype**: On *Lycopersicon esculentum* P. Miller, Mound City, Pulaski County, Illinois, 13.XI.1927, leg. G.L. Stout, ILLS 20939.

Metasphaeria asparagi L.R. Tehon & G.L. Stout, Mycologia 21:182–183. 1929. **Holotype**: On *Asparagus officinalis* L., Anna, Union County, Illinois, 11.XI.1926, leg. G.L. Stout, ILLS 19944.

Metasphaeria sassafrasicola L.R. Tehon & G.L. Stout, Mycologia 21:183. 1929. **Holotype**: On *Sassafras albidum* (T. Nuttall) C.G. Nees von Esenbeck, Seymour, Champaign County, Illinois, 15.X.1925, leg. L.R. Tehon, ILLS 20103 [as *S. variifolium* (R.A. Salisbury) O. Kuntze in protologue].

Microstroma pithecolobii E.M.R. Lamkey *in* F.L. Stevens, Mycologia 12:52. 1920. **Isotype**: On *Samanea saman* (N.J. Jacquin) E.D. Merrill [as *Pithecollobium saman* (N.J. Jacquin) G. Bentham], Mayaguez, Puerto Rico, XII.1913, leg. F.L. Stevens 6734, ex 70896, ILLS 41770.

Mollisia lithocarpi E.K. Cash, Mycologia 50:647–648. 1958. **Isotype**: On dead leaves attached to fallen branches of *Lithocarpus densiflora* (W.J. Hooker & G. Arnott) A. Rehder, Big Basin State Park, Santa Cruz County, California, 15.VII.1954, leg. L. Bonar, ILLS 40594.

Monodictys cruciseptata J.L. Crane & J.D. Schoknecht, Canadian Journal of Botany 61:2244–2247. 1983. **Holotype**: On submerged sticks incubated on filter paper, also on filter paper, Shark Valley, Everglades National Park, Florida, 3.III.1976, leg. J.L.Crane & J.D. Schoknecht, ILLS 42713.

Mycosphaerella cornicola L.R. Tehon & E.Y. Daniels, Mycologia 17:240–241. 1925. **Holotype:** On bark of *Cornus stolonifera* A. Michaux, Apple River Canyon, Jo Daviess County, Illinois, 17.VII.1924, leg. P.A. Young, ILLS 13596.

Mycosphaerella holci L.R. Tehon, Mycologia 29:434–435. 1937. **Holotype**: On living leaves of *Sorghum vulgare* C.H. Persoon var. *technicum* (F.A. Körnicke) O. Stapf ex J.H. Holland, Oakland, Coles County, Illinois, 5.X.1927, leg. G.L. Stout, ILLS 11591. **Paratype**: Mattoon, Coles County, Illinois, 5.X.1927, leg. G.L. Stout, ILLS 11682.

Mycosphaerella juglandis K.J. Kessler, Mycologia 76:363. 1984. **Isotype**: On *Juglans nigra* L., SW½ Sec. 28, T14S, R2W, Alexander County, Illinois, 23.V.1979, leg. K.J. Kessler, ILLS 42084.

Mycosphaerella zeicola G.L. Stout, Mycologia 22:278–279. 1930. **Holotype**: On *Zea mays* L., Vandalia, Fayette County, Illinois, 6.XI.1926, leg. G.L. Stout, ILLS 13803. **Paratypes**: Belleview, Calhoun County, Illinois, 7.XI.1927, leg. G.L. Stout, ILLS 21154; Bruce, Moultrie County, Illinois, 21.X.1927, leg. G.L. Stout, ILLS 21194; Champaign County, Illinois, 23.IX.1927, leg. G.L. Stout, ILLS 21151; Effingham, Effingham County, Illinois, 20.IX.1927, leg. G.L. Stout, ILLS 21166; Gibson City, Ford County, Illinois, 4.X.1926, leg. G.L. Stout, ILLS 19697; Harrisburg, Saline County, Illinois, 10.X.1927, leg. G.L. Stout, ILLS 21212; Mattoon, Coles County, Illinois, 15.IX.1927, leg. G.L. Stout, ILLS 21164; Minonk, Woodford County, Illinois, 29.IX.1926; leg. G.L. Stout, ILLS 19685; McLeansboro, Hamilton County, Illinois, 10.XI.1926, leg. G.L. Stout, ILLS 20136;

Mt. Carmel, Wabash County, Illinois, 6.X.1927, leg. G.L. Stout, ILLS 21222; Riverton, Sangamon County, Illinois, 19.X.1927, leg. G.L. Stout, ILLS 21216; West City, Franklin County, Illinois, 12.XI.1926, leg. G.L. Stout, ILLS 19629.

Nais glitra J.L. Crane & C.A. Shearer, Transactions of the British Mycological Society 86:509. 1986. **Holotype**: Red mangrove wood (*Rhizophora mangle* L.), submerged in Coot Bay, Everglades National Park, Florida, 14.III.1984, leg. J.L. Crane & C.A. Shearer CS-720-1, ILLS 44900.

Nakataea serpens C.A. Shearer & J.L. Crane, Transactions of the British Mycological Society 73:370. 1979. **Holotype**: Isolated from plant debris collected from Quiver Creek, Mason County, Illinois, 11.VIII.1978, leg. C.A. Shearer, ILLS 38410. **Isotype**: ILLS 42909, culture from the type: ATCC 38018.

Neta lignicola C.A. Shearer, Mycologia 66:21–23. 1974. **Holotype**: On balsa wood [*Ochroma pyramidale* (A.J. Cavanilles) I. Urban] submerged in Patuxent River at Triadelphia Reservoir, Brighton, Maryland, 22.VII.1969, leg. C.A. Shearer CS-223, ILLS 35536.

Neta patuxentica C.A. Shearer & J.L. Crane, Mycologia 63:241–242. 1971. **Holotype**: Isolated from balsa wood [*Ochroma pyramidale* (A.J. Cavanilles) I. Urban] submerged in the Patuxent River at the Patuxent Wildlife Refuge Center, U.S. Department of Interior, Laurel, Maryland, U.S.A., 10.X.1967, leg. C.A. Shearer & J.L. Crane A-64, ILLS 34520. **Paratypes**: DAOM 127056, ILLS 34827; DAOM 127053, ILLS 34809; DAOM 127057, ILLS 34828; DAOM 127054, ILLS 34825; DAOM 127055, ILLS 34826, culture from the type: ATCC 18854.

Nitschkia polygoni L.R. Tehon & E.Y. Daniels, Mycologia 19:111. 1927. **Holotype**: On *Polygonum* sp., Villa Ridge, Pulaski County, Illinois, 21.VI.1925, leg. P.A. Young, ILLS 9239.

Parasympodiella minima J.L. Crane & J.D. Schoknecht, Canadian Journal of Botany 60:369. 1982. **Holotype**: On submerged, decayed plant material, cypress swamp, Florida Route 6, Hamilton County, Florida, 17.V.1977, leg. J.L. Crane & J.D. Schoknecht, ILLS 39789.

Paratomenticola georgiana J.L. Crane & J.D. Schoknecht, Canadian Journal of Botany 60:369–371. 1982. **Holotype**: On a dead frond of *Serenoa repens* (W. Bartram) J.K. Small, Monkey Lake Landing, Suwannee Canal, Okefenokee National Wildlife Refuge, Georgia, 28.VIII.1978, leg. J.L. Crane & J.D. Schoknecht, ILLS 39897. **Isotype**: NY.

Pestalozzia heucherae L.R. Tehon & E.Y. Daniels, Mycologia 19:126–127. 1927. **Holotype**: On *Heuchera parviflora* F.G. Bartling, Fountain Bluff, Jackson County, Illinois, 20.VI.1924, leg. P.A. Young, ILLS 2873.

Phacidium negundinis L.R. Tehon & E.Y. Daniels, Mycologia 17:240. 1925. **Holotype**: On diseased twigs of *Acer negundo* L., Urbana, Champaign County, Illinois, 3.VI.1922, leg. P.A. Young, ILLS 8890.

Phaeocytosporella zeae G.L. Stout, Mycologia 22:280–281. 1930. **Holotype**: On culms of *Zea mays* L., Mattoon, Coles County, Illinois, 19.X.1926, leg. G.L. Stout, ILLS 20039.

Phaeoseptoria caricis L.R. Tehon & E.Y. Daniels, Mycologia 17:245. 1925. **Holotype**: On leaves of *Carex* sp., Ursa, Adams County, Illinois, 28.VI.1922, leg. O.A. Plunkett, ILLS 15455.

Phialocephala fluminis C.A. Shearer, J.L. Crane, & M.A. Miller, Mycologia 68:186–188. 1976. **Holotype**: On balsa wood [*Ochroma pyramidale* (A.J. Cavanilles) I. Urban] submerged in the Sangamon River, Station 15, at Decatur, Macon County, Illinois, 15.IV.1975, leg. C.A. Shearer & J.L. Crane 466-1, ILLS 36160. **Isotype**: NY, culture from the type: ATCC 32105.

Phialocephala illini J.L. Crane, Transactions of the British Mycological Society 56:162–163. 1971. **Holotype**: On decayed wood of *Taxodium disticum* (L.) L.C. Richard, Elvira Cypress Swamp, northwest of Vienna, Johnson County, Illinois, 18.XI.1969, leg. J.L. Crane 202-69, ILLS 34911.

Phoma asparagina L.R. Tehon & G.L. Stout, Mycologia 21:187. 1929. **Holotype**: On *Asparagus officinalis* L., Anna, Union County, Illinois, 11.XI.1926, leg. G.L. Stout, ILLS 19943.

Phomopsis callistephi L.R. Tehon & E.Y. Daniels, Mycologia 17:242. 1925. **Holotype**: On stems of *Callistephus hortensis* (L.) C.G. Nees von Esenbeck, Shelbyville, Shelby County, Illinois, 20.IX.1924, leg. P.A. Young, ILLS 2014.

Phomopsis ganjae J.M. McPartland, Mycotaxon. An International Journal Designed to Expedite Publication of Research on Taxonomy & Nomenclature of Fungi & Lichens 18:527–528. 1983. **Holotype**: On living leaves of *Cannabis sativa* L., Hanna City, Peoria County, Illinois, 8.VIII.1982, leg. P.L. Pruitt & J.M. McPartland, ILLS 43621.

Phyllachora cinnae L.R. Tehon & E.Y. Daniels, Mycologia 19:110–111. 1927. **Holotype**: On *Cinna arundinacea* L., Granite City, Madison County, Illinois, VIII.1924 [as 1920 in original publication], leg. P.A. Young, ILLS 9316.

Phyllosticta allegheniensis L.R. Tehon & G.L. Stout, Mycologia 21:185. 1929. **Holotype**: On *Rubus allegheniensis* T.C. Porter, Nashville, Washington County, Illinois, 29.VII.1926, leg. G.L. Stout, ILLS 20940.

Phyllosticta allii L.R. Tehon & E.Y. Daniels, Mycologia 17:241–242. 1925. **Holotype**: On *Allium cepa* L., Columbia, Monroe County, Illinois, 24.VIII.1922, leg. P.A. Young, ILLS 11132.

Phyllosticta anserinae L.R. Tehon, Mycologia 25:243. 1933. **Holotype**: On living leaves of *Potentilla anserina* L., Witt, Montgomery County, Illinois, 23.VI.1927, leg. G.L. Stout, ILLS 22762.

Phyllosticta aquilegiae L.R. Tehon & E.Y. Daniels, Mycologia 17:241. 1925. **Holotype**: On leaves of *Aquilegia canadensis* L., Marion, Williamson County, Illinois, 19.VII.1922, leg. P.A. Young, ILLS 2098.

Phyllosticta atomata L.R. Tehon, Mycologia 29:437. 1937. **Holotype**: On living leaves of *Plantago rugelii* J. Decaisne, Elizabeth, Jo Daviess County, Illinois, 24.VII.1927, leg. L.R. Tehon, ILLS 10349.

Phyllosticta avenophila L.R. Tehon & E.Y. Daniels, Mycologia 19:118–119. 1927. **Holotype**: On *Avena sativa* L., Piper City, Ford County, Illinois, 19.VI.1925, leg. L.R. Tehon, ILLS 2415.

Phyllosticta chenopodiicola L.R. Tehon & E.Y. Daniels, Mycologia 19:121. 1927. **Holotype**: On *Chenopodium album* L., Lincoln, Logan County, Illinois, 22.VII.1925, leg. L.R. Tehon, ILLS 6309. **Paratypes**: Mason City, Mason County, Illinois, 22.VII.1925, leg. L.R. Tehon, ILLS 10190; Nashville, Washington County, Illinois, 13.VIII.1925, leg. L.R. Tehon, ILLS 16667.

Phyllosticta circuligerens L.R. Tehon & E.Y. Daniels, Mycologia 19:120–121. 1927. **Holotype**: On *Rumex altissimus* A. Wood, Dongola, Union County, Illinois, 12.VIII.1922, leg. P.A. Young, ILLS 1007.

Phyllosticta dispergens L.R. Tehon, Mycologia 25:242–243. 1933. **Holotype**: On leaves of *Rubus flagellaris* K.L. Willdenow, Belleville, St. Clair County, Illinois, 9.VIII.1927, leg. G.L. Stout, ILLS 829.

Phyllosticta glycineum L.R. Tehon & E.Y. Daniels, Mycologia 19:117. 1927. **Holotype**: On *Glycine hispida* C.J. Maximowicz [=*G. max* (L.) E.D. Merrill], Arthur, Douglas County, Illinois, 6.VII.1925, leg. L.R. Tehon, ILLS 4392.

Phyllosticta gymnocladi L.R. Tehon & E.Y. Daniels, Mycologia 19:114. 1927. **Holotype**: On *Gymnocladus dioica* (L.) K. Koch, Lawrenceville, Lawrence County, Illinois, 27.VIII.1925, leg. L.R. Tehon, ILLS 10319.

Phyllosticta illinoensis L.R. Tehon & E.Y. Daniels, Mycologia 19:120. 1927. **Holotype**: On *Sassafras variifolium* (R.A. Salisbury) O. Kuntze [=*S. albidum* (T. Nuttall) C.G. Nees von Esenbeck], Grand Tower, Jackson County, Illinois, 17.VIII.1922, leg. P.A. Young, ILLS 574. **Paratype**: Coxeyville, Monroe County, Illinois, 23.VIII.1922, leg. P.A. Young, ILLS 5096.

Phyllosticta menispermicola L.R. Tehon & E.Y. Daniels, Mycologia 19:119. 1927. **Holotype**: On *Menispermum canadense* L., Porterfield, Marshall County, Illinois, 24.VIII.1922, leg. C.L. Porter, ILLS 8038 [as 8039 in original publication].

Phyllosticta neuroterigallicola L.R. Tehon, Mycologia 25:240–241. 1933. **Holotype**: On leaves of *Quercus imbricaria* A. Michaux, Dongola, Union County, Illinois, 11.VIII.1927, leg. G.L. Stout, ILLS 22830.

Phyllosticta nymphaeicola L.R. Tehon & E.Y. Daniels, Mycologia 19:117. 1927. **Holotype**: On *Nuphar luteum* (L.) J. Sibthorp ssp. *macrophyllum* (J.K. Small) E.O. Beal [as *Nymphaea advena* (D.C. Solander) R. Brown in protologue], Olney, Richland County, Illinois, 28.VIII.1925, leg. L.R. Tehon, ILLS 11093.

Phyllosticta plantaginicola L.R. Tehon & E.Y. Daniels, Mycologia 19:118. 1927. **Holotype**: On *Plantago virginica* L., Marshall, Clark County, Illinois, 1.VII.1925, leg. L.R. Tehon, ILLS 3188.

Phyllosticta podophyllina L.R. Tehon & G.L. Stout, Mycologia 21:184–185. 1929. **Holotype**: On *Podophyllum peltatum* L., Columbia, Monroe County, Illinois, 24.VI.1926, leg. L.R. Tehon, ILLS 19480.

Phyllosticta porteri L.R. Tehon & E.Y. Daniels, Mycologia 19:113–114. 1927. **Holotype**: On *Syringa vulgaris* L., Oregon, Ogle County, Illinois, 26.VIII.1922, leg. C.L. Porter, ILLS 3097.

Phyllosticta pteleicola L.R. Tehon & E.Y. Daniels, Mycologia 17:241. 1925. **Holotype**: On leaves of *Ptelea trifoliata* L., Starved Rock, LaSalle County, Illinois, 27.VI.1924, leg. P.A. Young, ILLS 6807.

Phyllosticta rafinesquii H.W. Anderson, Transactions of the Illinois State Academy of Science 15:128–129. 1922. **Holotype**: On *Viola rafinesquii* E.L. Greene, Anna, Union County, Illinois, 23.IV.1921, leg. H.W. Anderson, ILLS 4724.

Phyllosticta rugelii L.R. Tehon & G.L. Stout, Mycologia 21:184. 1929. **Holotype**: On *Plantago rugelii* J. Decaisne, Lawrenceville, Lawrence County, Illinois, 27.VI.1926, leg. L.R. Tehon, ILLS 19477.

ticta scariolicola L.R. Tehon, Mycologia 25:245. 1933. **Holotype**: On living leaves of *Lactuca scariola* L., West Union, Clark County, Illinois, 8.VI.1927, leg. G.L. Stout, ILLS 22503.

Phyllosticta solidaginicola L.R. Tehon & E.Y. Daniels, Mycologia 19:116. 1927. **Holotype**: On *Solidago* sp., Sumner, Richland County, Illinois, 27.VIII.1925, leg. L.R. Tehon, ILLS 10114.

Phyllosticta zeae G.L. Stout, Mycologia 22:281–282. 1930. **Holotype**: On leaf of *Zea mays* L., Robinson, Crawford County, Illinois, 5.XI.1926, leg. G.L. Stout, ILLS 19359. **Paratypes**: DuQuoin, Perry County, Illinois, 8.IX.1927, leg. G.L. Stout, ILLS 21196; Mattoon, Coles County, Illinois, 15.IX.1927, leg. G.L. Stout, ILLS 21165.

Physalospora zeae G.L. Stout, Mycologia 22:282. 1930. **Holotype**: On leaves of *Zea mays* L., Vandalia, Fayette County, Illinois, 6.XI.1926, leg. G.L. Stout, ILLS 19883.

Pirostoma nyssae L.R. Tehon, Mycologia 16:137. 1924. **Holotype**: On *Nyssa sylvatica* Marsh., Tunnel Hill, Johnson County, Illinois, 25.VII.1922, leg. P.A. Young, ILLS 2940.

Placosphaeria medicaginis L.R. Tehon, Mycologia 31:538–539. 1939. **Holotype**: On *Medicago sativa* L., Freeburg, St. Clair County, Illinois, 22.X.1935, leg. G.H. Boewe, ILLS 25276. **Paratypes**: Malta, De Kalb County, Illinois, 17.VII.1936, leg. G.H. Boewe, ILLS 26977; Centralia, Marion County, Illinois, 29.IV.1938, leg. G.H. Boewe, ILLS 26704.

Pleosphaerulina zeicola G.L. Stout, Mycologia 22:284. 1930. **Holotype**: On leaf of *Zea mays* L., Highland, Madison County, Illinois, 26.X.1927, leg. G.L. Stout, ILLS 21182.

Pleospora aquatica D. Griffiths, Bulletin of the Torrey Botanical Club (and Torreya) 26:443. 1899. **Isotype**: On dead *Eleocharis palustris* (L.) J.J. Roemer & J.A. Schultes, Aberdeen, Brown County, South Dakota, V.1896, leg. D. Griffiths, ILLS 42699.

Pleospora oleraceae L.R. Tehon & G.L. Stout, Mycologia 21:183–184. 1929. **Holotype**: On *Brassica oleracea* L. var. *capitata* L., West Vienna, Johnson County, Illinois, 7.VII.1926, leg. G.L. Stout, ILLS 19358.

Podospora pectinata N. Lundqvist, Svensk Botanisk Tidskrift 64:417. 1970. **Paratype**: U.S.A. Colorado, Boulder County, west base of Mt. Steamboat at foothills of Front Range, 3 km northwest of Lyons, near mouth of St. Vrain [as Vain on label] Creek, altitude 1900 m, on old cow dung incubated in moist chamber at Uppsala, 30.IV.1966, leg. R. Santesson 18499-c, ILLS 35158, FH, IMI, TRTC, UC, UPS.

Pseudodictya sassafrasicola L.R. Tehon & G.L. Stout, Mycologia 21:192. 1929. **Holotype**: On *Sassafras varrifolium* (R.A. Salisbury) O. Kuntze [=*S. albidum* (T. Nuttall) C.G. Nees von Esenbeck], Seymour, Champaign County, Illinois, 15.X.1925, leg. L.R. Tehon, ILLS 9353.

Puccinia puritanica G.B. Cummins, Bulletin of the Torrey Botanical Club (and Torreya) 68:45. 1941. **Isotype**: On *Carex pensylvanica* J.B. Lamarck, Waltham, Massachusetts, 1.X.1910, leg. A.B. Seymour, ILLS 41662, BPI. **Holotype**: PUR.

Pyrenochaeta minuta J.C. Carter, Illinois Natural History Survey Bulletin 21(6):219. 1941. **Holotype**: On branch of *Quercus palustris* O. von Muenchhausen, Xenia, Clay County, Illinois, 8.X.1937, leg. J.C. Carter, ILLS 27082.

Rhizopogon oswaldii A.H. Smith *in* A.H. Smith and S.M. Zeller, Memoirs of the New York Botanical Garden, Bronx 14(2):107–108. 1966. **Paratype**: In an old horse corral, Mt. Wilson Road, Bear Springs, Mt. Hood National Forest, Wasco County, Oregon, 26.X.1946, leg. W.B. Gruber (A.H. Smith 25065), ILLS 44316.

Rhizopogon pinyonensis K.A. Harrison & A.H. Smith var. *pinyonensis*, Canadian Journal of Botany 46:890. 1968. **Paratype**: Under piñon pine, Hyde Park Road, near Santa Fe, Santa Fe County, New Mexico, 7.X.1967, leg. K.A. Harrison 7321, ILLS 44325.

Rhizopogon pseudoaffinis A.H. Smith *in* A.H. Smith and S.M. Zeller, Memoirs of the New York Botanical Garden 14(2):138–139. 1966. **Paratype**: Brundage Mountain, Valley County, Idaho, 8.VIII.1962, leg. A.H. Smith 65780, ILLS 44320.

Rhizopogon rubescens E.L.R. Tulasne var. *ochraceus* A.H. Smith, *in* A.H. Smith and S.M. Zeller, Memoirs of the New York Botanical Garden 14(2):99–100. 1966. **Paratype**: Under white pine bark and alpine fir, Heaven's Gate Ridge, Seven Devils Mountains, Idaho County, Idaho, 2.VIII.1958, leg. A.H. Smith 59481, ILLS 44315.

Rhodosticta quercina J.C. Carter, Illinois Natural History Survey Bulletin 21(6):223. 1941. **Holotype**: On branch of *Quercus palustris* O. von Muenchhausen, Onarga, Iroquois County, Illinois, 25.X.1935, leg. J.C. Carter, ILLS 27083.

Rogersia annelidica C.A. Shearer & J.L. Crane, Mycologia 68:949–950. 1976. ≡*Filosporella annelidica* (C.A. Shearer & J.L. Crane) J.L. Crane & C.L. Shearer, Mycotaxon 6:28. 1977. **Holotype**: On sycamore leaves (*Platanus occidentalis* L.) submerged in the Sangamon

River at Brigham Station No. 1, Mahomet, Champaign County, Illinois, 16.II.1976, leg. C.A. Shearer S-77-8, ILLS 36352. **Paratypes**: ILLS 36343, ILLS 36344, ILLS 36345, ILLS 36346, ILLS 36347, ILLS 36348, ILLS 36349, ILLS 36350, ILLS 36351, culture from the type: ATCC 32834.

Rogersiomyces okefenokeensis J.L. Crane & J.D. Schoknecht, American Journal of Botany 65:903. 1978. **Holotype**: On submerged, decayed leaves of angiosperms and *Taxodium* sp., Trembling Earth Nature Trail, Steven Foster State Park, Okefenokee National Wildlife Refuge, Georgia, 10.V.1976, leg. J.L. Crane & J.D. Schoknecht, ILLS 37095. **Isotype**: NY, culture from the type: ATCC 36118.

Rostrosphaeria phlei L.R. Tehon & E.Y. Daniels, Mycologia 19:112. 1927. **Holotype**: On *Phleum pratense* L., Jacksonville, Morgan County, Illinois, 25.VII.1925, leg. L.R. Tehon, ILLS 893.

Scolecobasidium cylindrosporum J.L. Crane & J.D. Schoknecht, Canadian Journal of Botany 60:372. 1982. **Holotype**: On submerged, decayed wood, Minnie's Lake, Okefenokee National Wildlife Refuge, Georgia, 17.V.1977, leg. J.L. Crane & J.D. Schoknecht, ILLS 40889.

Scolecobasidium salmonicolor C.A. Shearer, Mycologia 66:18–20. 1974. **Holotype**: On Cantino PYF agar, isolated from balsa wood submerged in the Patuxent River at Lower Marlboro, Maryland, 6.V.1969, leg. C.A. Shearer, CS-180, ILLS 35537, culture from the type: ATCC 24299.

Sebacina farinacea D.P. Rogers, Pacific Science 1:97. 1947. **Paratype**: On sheath of *Cocos nucifera* L., on campus, Mauoa, Oahu, Hawaii, 20.III.1946, leg. I.A. Abbott & D.P. Rogers (DPR 1175), ILLS 39247.

Sebacina petiolata D.P. Rogers, Pacific Science 1:99. 1947. **Paratypes**: On bark of *Acacia koa* A. Gray, Tautalus Tr., Pauoa (c. 1500 ft), Oahu, Hawaii, 21.VII.1946, leg. D.P. Rogers (DPR 1331), ILLS 39249. On *Cocos nucifera* L., fallen log, Ormed I., Wotje, Atoll, Marshall Islands, 4.IX.1946, leg. D.P. Rogers (DPR 1385), ILLS 39210.

Septocylindrium hydrophylli E.Y. Daniels, Mycologia 19:127. 1927. **Holotype**: On *Hydrophyllum canadense* L., Seymour, Champaign County, Illinois, 15.X.1925, leg. E.Y. Daniels, ILLS 9531.

Septogloeum equiseti L.R. Tehon, Mycologia 29:445–446. 1937. **Holotype**: On living stems of *Equisetum laevigatum* A. Braun, Sterling, Whiteside County, Illinois, 23.VII.1927, leg. L.R. Tehon, ILLS 10369.

Septoria atropurpurei L.R. Tehon, Mycologia 16:135–136. 1924. **Holotype**: On *Euonymus atropurpureus* N.J. Jacquin, Marion, Williamson County, Illinois, 19.VII.1922, leg. P.A. Young, ILLS 2064.

Septoria collinsiae H.W. Anderson, Transactions of the Illinois State Academy of Science 15:127. 1922. **Holotype**: On *Collinsia verna* T. Nuttall, Brownfield Woods, Urbana, Champaign County, Illinois, 18.V.1919, leg. H.W. Anderson, ILLS 4723.

Septoria cunillae L.R. Tehon, Mycologia 25:249–250. 1933. **Holotype**: On *Cunila origanoides* (L.) N.L. Britton, Alto Pass, Union County, Illinois, 13.VI.1927, leg. G.L. Stout, ILLS 22557.

Septoria eupatoriicola L.R. Tehon, Mycologia 25:250. 1933. **Holotype**: On leaves of *Eupatorium perfoliatum* L., DuQuoin, Perry County, Illinois, 13.VI.1930, leg. L.R. Tehon, ILLS 22260.

Septoria festucina L.R. Tehon & E.Y. Daniels, Mycologia 19:125–126. 1927. **Holotype**: On *Festuca elatior* L., Tallula, Menard County, Illinois, 16.VI.1922, leg. O.A. Plunkett, ILLS 9224.

Septoria pinicola J.B. Dearness, Mycologia 20:237. 1928. **Isotype**: On *Pinus virginiana* P. Miller, Chain Bridge, Virginia, 10.V.1927, leg. G.G. Hedgcock, communicated by Paul V. Siggers, ILLS 27098. **Holotype**: DAOM.

Septoria septentrionalis H.W. Anderson, Transactions of the Illinois State Academy of Science 15:127–128. 1922. **Holotype**: On lower leaves of *Ranunculus septentrionalis* J.L.M. Poiret, Brownfield Woods, Urbana, Champaign County, Illinois, 21.IV.1921, leg. H.W. Anderson, ILLS 4725.

Septoria tecomaxochitl L.R. Tehon & G.L. Stout, Mycologia 21:191. 1929. **Holotype**: On *Campsis radicans* (L.) B.C. Seemann ex Bureau [as *Tecoma radicans* (L.) A.L. de Jussieu in protologue], Lawrenceville, Lawrence County, Illinois, 20.X.1926 [as 26.X in protologue], leg. G.L. Stout, ILLS 20946.

Septoria zeae G.L. Stout, Mycologia 22:284–285. 1930. **Holotype**: On leaf of *Zea mays* L., Joliet, Will County, Illinois, 24.IX.1926, leg. G.L. Stout, ILLS 19673. **Paratypes**: Dixon, Lee County, Illinois, 27.IX.1926, leg. G.L. Stout, ILLS 19681; Elgin, Kane County, Illinois, 24.IX.1926, leg. G.L. Stout, ILLS 19725; Moline, Rock Island County, Illinois, 8.X.1926, leg. G.L. Stout, ILLS 19716; Mt. Carroll, Carroll County, Illinois, 27.IX.1926, leg. G.L.Stout, ILLS 19682; Rockford, Winnebago County, Illinois, 25.IX.1926, leg. G.L. Stout, ILLS 19677; Stockton, Jo Daviess County, Illinois, 27.IX.1926, leg. G.L.Stout, ILLS 19683; Streator, La Salle County, Illinois, 23.IX.1926, leg. G.L.Stout, ILLS 20100.

Septoria zeicola G.L. Stout, Mycologia 22:286. 1930. **Holotype**: On leaf of *Zea mays* L., Vandalia, Fayette County, Illinois, 6.X.1926, leg. G.L. Stout, ILLS 20102. **Paratypes**: Casey, Clark County, Illinois, 24.X.1927, leg. G.L. Stout, ILLS 21160; Harrisburg, Saline County, Illinois, 10.X.1927, leg. G.L. Stout, ILLS 21211; Mattoon, Coles County, Illinois, 15.IX.1927, leg. G.L. Stout, ILLS 21162; Toulon, Stark County, Illinois, 7.X.1926, leg. G.L. Stout, ILLS 20138; West City, Franklin County, Illinois, 12.XI.1926, leg. G.L. Stout, ILLS 19629.

Septoria zeina G.L. Stout, Mycologia 22:287. 1930. **Holotype**: On leaf of *Zea mays* L., Taylorville, Christian County, Illinois, 20.X.1927, leg. G.L. Stout, ILLS 21231.

Sirococcus phlei L.R. Tehon & E.Y. Daniels, Mycologia 19:122. 1927. **Holotype**: On *Phleum pratense* L., New Berlin, Sangamon County, Illinois, 25.VII.1925, leg. L.R. Tehon, ILLS 14799.

Sphaeropsis ampelopsidis E.Y. Daniels *in* L.R. Tehon & E.Y. Daniels, Mycologia 19:123–124. 1927. **Holotype**: On *Parthenocissus quinquefolia* (L.) J.L. Planchon [as *Ampelopsis quinquefolia* (L.) A. Michaux in original publication], Fisher, Champaign County, Illinois, 20.X.1925, leg. L.R. Tehon, ILLS 2541.

Sphaeropsis negundinis L.R. Tehon & E.Y. Daniels, Mycologia 17:242–243. 1925. **Holotype**: On diseased twigs of *Acer negundo* L., Urbana, Champaign County, Illinois, 3.VI.1922, leg. P.A. Young, ILLS 15198.

Sphaeropsis profundae L.R. Tehon & E.Y. Daniels, Mycologia 19:124. 1927. **Holotype**: On *Fraxinus profunda* (B.F. Bush) B.F. Bush [=*F. tomentosa* F.A. Michaux], Fountain Bluff, Jackson County, Illinois, 20.VI.1924, leg. P.A. Young, ILLS 17554.

Sporidesmium taxodii J.L. Crane, Transactions of the British Mycological Society 58:425–426. 1972. **Holotype**: On submerged decaying leaves of *Taxodium distichum* (L.) L.C. Richard, Elvira Cypress Swamp, northwest of Vienna, Johnson County, Illinois, 29.X.1969, leg. J.L. Crane 222-69, ILLS 34936. **Isotype**: NY.

Stagonospora heteroderae L.M. Carris, D.A. Glawe & G. Morgan-Jones, Mycotaxon. An International Journal Designed to Expedite Publication of Research on Taxonomy & Nomenclature of Fungi & Lichens 29:451–452. 1987. **Holotype**: Isolated from cyst of *Heterodera glycines*, Sidney, Champaign County, Illinois, 22.VIII.1985, leg. L.M. Carris, ILLS 46332, culture from the type: ATCC 62861.

Stagonospora scirpi L.R. Tehon, Mycologia 25:247–248. 1933. **Holotype**: On leaves and sheaths of *Scirpus atrovirens* K.L. Willdenow, DuQuoin, Perry County, Illinois, 13.VI.1930, leg. L.R. Tehon, ILLS 22259.

Stictopatella iridis L.R. Tehon, Mycologia 40:320–321. 1948. **Holotype**: On leaves of *Iris virginica* L. var. *shrevei* (J.K. Small) E. Anderson, Urbana, Champaign County, Illinois, 11.VI.1947, leg. R.A. Evers, ILLS 30048.

Stigmatea plantaginis L.R. Tehon & E.Y. Daniels, Mycologia 19:111–112. 1927. **Holotype**: On *Plantago virginica* L., Carthage, Hancock County, Illinois, 24.VII.1922, leg. O.A. Plunkett, ILLS 7652.

Stigmatophragmia sassafrasicola L.R. Tehon & G.L. Stout, Mycologia 21:181. 1929. **Holotype**: On *Sassafras variifolium* Kuntze, Seymour, Champaign County, Illinois, 15.X.1925, leg. L.R. Tehon, ILLS 21698.

Taeniolella americana J.L. Crane & J.D. Schoknecht, Canadian Journal of Botany 60:372–374. 1982. **Holotype**: On submerged, decayed ament of *Liquidambar styraciflua* L., Goose Pond, Johnson County, Illinois, 28.I.1974, leg. J.L. Crane, ILLS 41016.

Taeniolina deightonii J.L. Crane & J.D. Schoknecht, Mycologia 73:81–82. 1981. **Isotype**: On *Vismia guineensis* J.D. Choisy, Njala (Kori) Sierra Leone, 22.I.1951, leg. F.C. Deighton, [as *Torula herbarum*], ex **type material** M 3806, ILLS 42505. **Holotype**: IMI 45404.

Triadelphia heterospora C.A. Shearer & J.L. Crane, Mycologia 63:247–249. 1971. **Holotype**: On balsa wood [*Ochroma pyramidale* (A.J. Cavanilles) I. Urban] block submerged in the Patuxent River, Lower Marlboro, Maryland, 8.XII.1967, leg. C.A. Shearer & J.L. Crane A-33, ILLS 34793. **Isotypes**: DAOM 126798, ILLS 34793a, IMI 144033, NY. **Paratype**: Brighton Dam, Triadelphia Reservoir, Maryland, 5.I.1968, leg. C.A. Shearer and J.L. Crane, A-204, ILLS 34894, culture from the type: ATCC 22772.

Trichocladium linderi J.L. Crane & C.A. Shearer, Mycologia 70:866–869. 1978. **Holotype**: On balsa wood [*Ochroma pyramidale* (A.J. Cavanilles) I. Urban] blocks submerged in the Rhode River Estuary, Edgewater, Anne Arundel County, Maryland, 23.XI.1971, leg. C.A. Shearer CS-186-9, ILLS 37019. **Isotype**: NY. **Paratypes**: ILLS 37042, ILLS 37043.

Trichocladium moenitum J.L. Crane & C.A. Shearer, Mycologia 70:871. 1978. **Holotype**: On submerged decayed wood and filter paper in petri dish, Elvira Cypress Swamp (Deer Pond), Johnson County, Illinois, 21.III.1975, leg. J.L. Crane & C.A. Shearer 588-1, ILLS 36986. **Isotype**: NY. **Paratype**: ILLS 37028.

Triposporium batistae J.L. Crane & K.P. Dumont, Canadian Journal of Botany 53:844–845. 1975. **Isotype**: Saprophytic on a decayed pod (?), along the Rio Nueve Pasos, Dr. Luis Roure's property near Rosario, Puerto Rico, elevation 140 m, 17.VI.1970, leg. R.P. Korf et al., ILLS 34960. **Holotype**: NY. CUP-PR-4179, ILLS 4179.

Tripterospora latipes N. Lundqvist, Botaniska Notiser 122:592–593. 1969. ≡*Zopfiella latipes* (N. Lundqvist) D. Malloch & R.F. Cain, Canadian Journal of Botany 49:876. 1971. **Isotype**: Denmark, Sjaelland: Kjøbenhavn, Botanical Garden, isolated from compost soil from a greenhouse, 26.II.1968, leg. A. Kjoller, ILLS 35139. **Paratype**: ILLS 34539. **Holotype**: UPS.

Tubercularia ulmea J.C. Carter, Phytopathology 37:246. 1947. **Holotype**: On branches and trunks of *Ulmus pumila* L., Onarga, Iroquois County, Illinois, 16.VIII.1939, leg. J.C. Carter, ILLS 29559.

Vanbeverwijkia spirospora V. Agnihothrudu, Transactions of the British Mycological Society 44:53. 1961. **Isotype**: On decaying wood, Jorhat, Assam, India, 18.VIII.1958, leg. H.K. Phukan 168, ILLS 34901 as a microscopic preparation from HCIO. **Holotype**: Mycological Herbarium, Tocklai Experiment Station, Assam, India.

Varicosporium giganteum J.L. Crane, American Journal of Botany 55:999. 1968. **Isotypes**: From a foam sample, Androscoggin River, Errol, Coos County, New Hampshire, 5.IX.1966, leg. J.L. Crane 190C-66, ILLS 34469, ILLS 39803, ILLS 39940. Holotype: NY, culture from the type: ATCC 18147.

Verticillium rhizophagum L.R. Tehon & H.L. Jacobs, Bulletin of the Davey Tree Expert Company 6:16. 1936. **Holotype**: On *Ulmus americana* L., Dayton, Ohio, IX.1934, leg. P.R. Grimes, ILLS 28858.

Zopfiella lundqvistii C.A. Shearer & J.L. Crane, Transactions of the British Mycological Society 70:456. 1978. **Holotype**: A dried culture isolated from balsa wood and blocks (*Ochroma pyramidale* (A.J. Cavanilles) I. Urban), submerged in Elvira Cypress Swamp (Deer Pond), Johnson County, Illinois, 28.VI.1974, leg. C.A. Shearer & J.L. Crane CS-460-1, ILLS 36931. **Isotype**: NY, culture from the type: ATCC 34976..

Zygorrhynchus verruculosus L.R. Tehon, Transactions of the Illinois State Academy of Science 36:109–110. 1943. **Holotype**: Isolated from dead elm roots (*Ulmus americana* L.) , Peoria, Peoria County, Illinois, Summer 1941, leg. E.P. Metcalfe, ILLS 28927.

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Appendix. Type Specimens Missing from ILLS Herbarium

Name	Holotype (Accession number)	Paratype (Accession number)
Actinothyrium gloesporioides L.R. Tehon	2972	3671
Cryptostictis inaequalis L.R. Tehon & G.L. Stout	13698	
Macrophoma smilacinae L.R. Tehon & G.L. Stout	20001	
Macrophoma zeae L.R. Tehon & E.Y. Daniels	1247	

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